Quantifying Biodiversity in Farmland and Detecting its Drivers

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CONTENTS

GENERAL INTRODUCTION

Biodiversity in farmland is an essential public good. However, it is hard to measure biodiversity and to assess the detailed consequences of agricultural production on it. To enhance knowledge on biodiversity in farmland it is necessary to survey, quantify and map the components of biological diversity. This PhD thesis investigates biodiversity in farmland at the species level. The investigations are based on plants, earthworms, spiders and bees (wild bees) at the habitat, farm and regional scale in a European context. To communicate findings on species diversity to farmers, appropriate metrics are recommended.

1. Biodiversity in Farmland

The term biodiversity comprises "the variability among living organisms from all sources (...) and the ecological complexes of which they are part" (Magurran, 2003). Biodiversity comprises a hierarchical system of different levels (such as genetic diversity, species diversity and habitat diversity; Noss, 1990). In Europe, a substantial amount of biodiversity, an estimated 50% of all wild species, is linked to farmland, which is one of the main land uses (Kristensen, 2003; EEA, 2010). In previous centuries, agriculture has contributed to biodiversity enhancement, e.g. by creating additional habitats and breeding new varieties (van Elsen, 2000). However, the intensification of agricultural production in the last decades has led to a decline and loss of biodiversity (e.g.Robinson and Sutherland, 2002). This is not only a loss regarding the intrinsic value of biodiversity but also a threat to the provision of crucial ecological functions (e.g. Loreau et al., 2002). Decomposition of organic material, pest predation and pollination are examples of such functions. To maintain and promote biodiversity, agricultural policy has implemented agri-environmental schemes. However, these schemes were not generally successful as studies of Bengtsson et al. (2005), Kleijn et al. (2006), Aviron et al. (2009) and Batáry et al. (2011) have shown. Agri-environmental

schemes differ in their effects among organism groups. Often they are beneficial to common but not to rare species. Additionally, landscape complexity, type of landscape and general intensity level influence the efficiency of agri-environment schemes. These multifaceted interactions make it difficult to ensure general benefits of agri-environmental schemes. Presumably, not the least due to this fact, farmers often lack motivation to apply measures which promise to benefit biodiversity (Gorton et al., 2008; Guillem and Barnes, 2013). Therefore, a better knowledge of the current state of biodiversity and of its interactions with abiotic and biotic factors in farmland at different spatial scales is needed. Such knowledge allows the detection of general and specific patterns and hinders further negative effects on farmland biodiversity (Heywood and Watson, 1995).

2. Measuring Biodiversity

"Inventorying of biodiversity is the fundamental starting point for its conservation, sustainable use and management" (Heywood and Watson, 1995). Thus, our knowledge of biodiversity depends on how it is measured. Measuring biodiversity requires specific approaches. This is because high demands on financial resources and insufficient systematic expertise for many groups of organisms hinder a comprehensive census of biodiversity. Noss (1990) proposed to subdivide biodiversity in hierarchical levels, compositions and functions. This enables focus to be placed on specific components of biodiversity and to combine these afterwards within a more complex framework. Depending on the question and the goal of the biodiversity investigation, the appropriate spatial and temporal scales must be addressed (Heywood and Watson, 1995). The combination of individual pieces of the puzzle increasingly contributes to an overall picture of biodiversity (Gaston, 1996). To allow such combinations and comparisons across several studies, the use of standardized sampling and analytical techniques is crucial (Heywood and Watson, 1995). Nevertheless, one has to be

aware that a quantification of biodiversity reported in an absolute number cannot be meaningfully interpreted unless described and analysed within a concrete spatial and temporal context, comparing like with like (Gaston, 1996). This issue further demands a differentiated and adapted communication of the findings of biodiversity investigations.

3. The BioBio Project

A common way to gain information about an entity that cannot be measured per se in total is the use of indicators. Such an entity, for which an approach by indicators is appropriate, is biodiversity (Büchs, 2003b; Duelli and Obrist, 2003). BioBio is a research project that proposed and evaluated a set of biodiversity indicators for European farming systems (Biodiversity indicators for organic and low-input farming systems, EU FP7, KBBE-227161, 2009 – 2012). The aim of the project was to identify a set of biodiversity indicators which are (i) scientifically and analytically sound, (ii) generic at the European scale and (iii) relevant and useful for stakeholders (Herzog et al., 2012). For that, a set of previously selected candidate indicators was tested in 13 case study regions across Europe and additionally in Tunisia and Uganda. Depending on the case study region, typical farm types were investigated: field crop & horticulture, specialist grazing livestock, mixed crop & livestock and permanent crop farms. Important criteria for testing the individual indicators were how easy and reliable they were applicable at the European scale and how well they could distinguish between farms. If indicators were correlated and did not provide additional information, the most meaningful was selected and the other(s) discarded. The complete biodiversity indicator set consisted of 23 core indicators. Three indicators focused on the genetic diversity, four indicators on species diversity, and eight indicators on habitat diversity of farms. Additionally, eight indicators reported on agricultural management that were

indirectly linked to biodiversity. This thesis relies on data that were collected in the BioBio project.

4. Indicators for Biodiversity at Species Level

To provide insight in the species level of biodiversity, scientific literature on various taxonomic groups was reviewed to collect candidate indicators in the BioBio project. The candidate indicators were classified accordingly to general criteria that biodiversity indicators should ideally meet (see e.g. Noss, 1990; Heywood and Watson, 1995). Subsequently, in collaboration with a stakeholder advisory board, the set of candidate indicators was reduced to four taxonomic groups, which were tested in the BioBio case study regions. These were vascular plants, earthworms, spiders and bees (wild bees).

Vascular plants are primary producers, relatively easy to identify and are reported to correlate reasonably well with overall organismic diversity (Duelli and Obrist, 1998). As sessile organisms, they are suitable indicators for long-term changes in management and environmental conditions (Perner and Malt, 2003). Earthworms contribute considerably to soil structure and soil fertility as decomposers (Paoletti, 1999a) and are known to be sensitive, e.g. to tillage practices and soil contents (Edwards and Bohlen, 1996; Pfiffner and Luka, 2007). Although this taxonomic group consists of relatively few species, they are widespread and can be collected with simple techniques. Spiders play an important role as predators and contribute to pest control in agro-ecosystems (Symondson et al., 2002; Nyffeler and Sunderland, 2003). They depend on vegetation structure and are quite mobile (Gibson et al., 1992; Weyman et al., 2002). Spiders have been found to be related to management practices and landscape structures in previous studies (Jeanneret et al., 2003; Clough et al., 2005; Schmidt et al., 2005). Species of this abundant taxonomic group occur in (nearly) all terrestrial ecosystems (Marc et al., 1999). The taxonomy of European spiders is well known

and allows reliable identification (Platnick, 2009). Wild bees (incl. bumblebees) contribute to a further important ecological function, the pollination (Klein et al., 2007). This taxonomic group is highly mobile, requires sufficient nectar and pollen supply, and appropriate nesting conditions (Tscharntke et al., 1998; Kremen et al., 2007; Zurbuchen et al., 2010). Pesticides applications and habitat composition have been shown to affect bee communities (Steffan-Dewenter et al., 2002; Mandelik et al., 2012; Whitehorn et al., 2012).

The four selected groups were complementary in the biotopes that they occupy, in their resource requirements and their trophic levels. Therefore, they had the potential to represent a broad spectrum of species diversity. Indeed, the evaluation of the four candidate indicators revealed contrasting responses and a lack of consistent correlations between the taxonomic groups. Therefore, in the BioBio project all four groups were retained and included in the final indicator set.

5. Measuring Biodiversity at Species Level

The study of species diversity, as one level of biodiversity, basically starts with the question: How many and which species were found at a specific site at a certain time? Mostly, such studies proceed with the assumption that samples are randomly collected from the community of interest (Magurran and McGill, 2011). However, the detectability of individuals and species varies considerably and this needs to be addressed appropriately (through methodological or mathematical processes) when conducting studies on communities of species. Communities can be described by the number of individuals or species, as well as by species composition, i.e. the relative abundance of species at a site. Therefore, the communities of different sites can be compared in several ways. Many different measurements exist to describe communities. Each of them focuses on a certain community component and measures particular properties. They are used to detect patterns among sites

and relationships between communities of species and environmental variables. Depending on the study question and its aim, as well as the temporal and spatial scale, the application of specific measurements and combinations of measurements are appropriate (Magurran, 2003).

5.1. Measurements for Different Components of Communities of Species

Abundance: The cover of species (e.g. plants), the biomass or the number of individuals, provides information about the amount/number of organisms that occur.

Species richness: The number of species is one of the most often used measurements to report on communities. Besides the observed species richness, estimated species richness values can be applied to account for unbalanced samples and unseen species. Common richness estimators are based on species-area or species-accumulation curves, such as e.g. Chao- or Jackknife-estimators (Magurran, 2003; Chao et al., 2005). An alternative to allow direct comparisons of the species richness of communities is the rarefaction technique (Gotelli and Colwell, 2001). Thereby data of different units are reduced to a common abundance level or sample number.

Species evenness indices: Measurements that focus exclusively on the distribution of species within a sample form the group of species evenness indices, such as the Berger-Parker- or the Smith and Wilson's evenness-index. Species evenness indices have specific characteristics regarding their sensitivity to species richness or their symmetry between abundant and rare species (Smith and Wilson, 1996; Magurran, 2003).

Species diversity indices: In the strict scientific sense, diversity consists of two components, richness, i.e. how many different species occur, and evenness, i.e. how evenly are the different species distributed (Büchs, 2003a). Species diversity indices combine these two components by accounting for the number of species as well as the relative abundance of each species. A variety of indices are available (e.g. Shannon- or Simpson-index) that differ in weighting

abundant and rare species, respectively (Jost, 2006). A comprehensive approach to species diversity measurements is provided by the family of Hill numbers. These numbers are expressed in directly comparable units of so called effective numbers of species. The list of Hill numbers forms "a mathematically unified family of diversity indices (differing among themselves only by an exponent q) that incorporate relative abundance and species richness" (Chao et al., 2014). For example, the observed species richness is a Hill number with $q = 0$.

Species composition (species assemblages): The most detailed information on communities is contained in species composition, i.e. the record of each individual or species (abundance or incidence data, respectively) per site. Species composition data are not single numbers but whole matrices that need to be analysed with multivariate techniques.

α, β and γ diversity: Whittaker (1960) established the concept of β diversity. He defined β diversity as the variation in species composition among sites in a geographical area. In this concept, α diversity describes the species diversity of a single site and γ diversity describes the total species diversity in the geographical area. To indicate β diversity, different approaches and indices were developed that combined α diversity and β diversity either in an additive or a multiplicative way to get γ diversity (Jost, 2007). Generally, β diversity is calculated directly from species-abundance (or –incidence) data, e.g. the Jaccard, Sørensen or Morisita-Horn index. The calculation of these indices differs in the weighting of species that are shared by two sites or that occur exclusively in one site (Magurran and McGill, 2011). Jost (2007) and Tuomisto (2010) carefully disentangled indices and the underlying concept of β diversity to make transparent the different components of diversity. If, at a higher level, the variation in the variation of species composition among groups of sites should be studied (i.e. variation in β diversity), the sites have to be displayed in a dissimilarity matrix and

calculations follow a distance approach (Legendre et al., 2005; Tuomisto and Ruokolainen, 2006). Again, depending on the study context the appropriate β diversity should be selected.

6. Drivers of Plant, Earthworm, Spider and Bee Communities

Agricultural management and landscape structure highly impact farmland species diversity. To assess such impacts, numerous studies have investigated, e.g. the effects of fertilizing, pest control or mechanical techniques and spatial arrangements of habitats on species diversity (Clough et al., 2005; Tscharntke et al., 2005; Concepción et al., 2012b). Multi-taxon research often included different arthropod groups (Oertli et al., 2005; Schweiger et al., 2005; Knop et al., 2006), but investigations on a combination of contrasting taxonomic groups across different regions are still rare (Gabriel et al., 2010; Concepción et al., 2012a; Báldi et al., 2013).

A general finding of recent research are the negative effects on farmland species diversity by high fertilization (e.g. mineral nitrogen), pesticides or high grazing pressure combined with a decrease in habitat diversity (Paoletti, 1999a; Batáry et al., 2008; Schmidt-Entling and Dobeli, 2009; Brittain et al., 2010; Gaba et al., 2010; Nieminen et al., 2011; Concepción et al., 2012b; Hinners et al., 2012). However, regional preconditions, landscape characteristics and taxonomic groups co-determined the amount of the effect (Kleijn et al., 2009; Batáry et al., 2010). Thus, large scale species surveys of contrasting taxonomic groups are important to disentangle general from specific effects. Such studies should allow priorities to be defined in different regions, in order to halt the loss of species diversity and to implement appropriate measures that benefit biodiversity (Gabriel et al., 2010; Concepción et al., 2012a).

7. The Issue of Scale

Species diversity surveys are undertaken in the area inhabited by the taxonomic group under investigation, i.e. in the respective habitat. Consequently, species were sampled at the habitat

scale in the BioBio project. Subsequently, to allow conclusions on farmland in general, species diversity was analysed at three scales: habitat, farm and region. Different community measurements were derived from the species abundance lists for each habitat. These measurements were then scaled up to the farm and region scale. To ensure a reliable up-scaling procedure, an appropriate sampling design and standardized sampling methods were applied (Gaston, 1996; Magurran, 2003). A stratified sampling design was applied: each farm was mapped and separated into different habitat types based on Raunkiær plant life forms, environment and management variables (Raunkiaer, 1934; Bunce et al., 2008). These habitat types included both, productive areas, such as e.g. crop fields, and non-productive areas which were affected by farming practices, such as e.g. hedgerows. Of each habitat type per farm, one was randomly selected for plant, earthworm, spider and bee sampling. This means, the separation of habitats took place at the same scale for all four taxonomic groups independent of their activity radius. An advantage of this approach was that comparisons across groups were possible, because the sampling was undertaken within the same boundaries for all four groups. Nevertheless, a disadvantage was that the habitat definitions might not have perfectly fitted to the resource requirements and exploitations of all species in the four groups. Further, the number of sampled habitats varied among farms as it was defined by the number of different habitat types recognized on the farm. Farms are rather economic than ecological units. They can differ in size and spatial organisation. For example, fields of an individual farm may be intermingled with fields managed by other farmers or non-farmed areas. These particular characteristics had to be taken into account by investigating and aggregating species diversity measurements at the farm scale. A second challenge was the geographical extent of the study to different regions across Europe and beyond, from Norway to Uganda and from Spain to Ukraine. In such large-scale surveys many persons are involved, who may have different skills. Therefore, the quality of species recognition, discrimination

and taxonomic identification can differ and influence species lists (Gaston, 1996). Hence, in all case study regions of the BioBio project, species of all four taxonomic groups (except earthworms in Tunisia and spiders in Uganda) were sampled according to standardized protocols, counted and identified by specialists (Dennis et al., 2012). The data were then centralised, checked and prepared. This included the control of habitat definitions, adaptations to the European nomenclature and the exclusion of juvenile earthworm and spider individuals. These preparations allowed the calculation of different community measurements.

8. Study Aims

In order to contribute additional pieces to the current knowledge on biodiversity, the aim of this study was to investigate plants, earthworms, spiders and bees (wild bees) in farmland of different European regions.

The main underlying questions were: what are similarities and differences in plant, earthworm, spider and bee communities in European farmland? how do communities of the four taxonomic groups respond to agricultural management? and, how are these responses related to effects of geographic location and surrounding landscape?

Firstly, focus was placed exclusively on productive arable and grassland fields. Secondly, non-productive habitats were included in the analyses. Species diversity was quantified at several scales, i.e. habitat, farm and regional scale, to separate general from specific patterns. Thirdly, appropriate ways to provide information for the enhancement of species diversity in farmland and for communication about species diversity with farmers in their sphere of influence were compiled.

SUMMARY

In this thesis, species diversity, a fundamental component of farmland biodiversity, was investigated. For this task, four contrasting taxonomic groups were selected: plants, earthworms, spiders and bees. The four taxonomic groups were sampled in 205 farms of ten European and two African regions as part of the BioBio project. They were inventoried and analysed with regard to three objectives. Firstly, to detect trends in species communities across a range of farming systems. Secondly, to examine the contrasting responses of the four taxonomic groups to agricultural management as well as landscape characteristics. This was undertaken for several regions at the habitat and farm scale. Thirdly, to propose a way to communicate findings on species diversity at farm scale which can form a basis for decision making.

In the study of **Chapter 1**, plants, earthworm, spider and bee communities in 167 arable fields of four regions were analysed. Abundance, species richness and species composition were considered as three complementary community aspects. By means of variation partitioning, we estimated the percentage of variation in communities explained by factors of three groups: (i) geographic location, (ii) agricultural management and (iii) surrounding landscape in a 250 m buffer zone. Whereas geographic location had a predominant effect on all communities, agricultural management also had a significant, independent effect on plants, spiders and bees. However, surrounding landscape factors had minor effects on the communities. Generally, mineral nitrogen input and pesticide applications decreased abundance and species richness, whereby each of the four taxonomic groups responded individually to agricultural management and surrounding landscape.

For the study in **Chapter 2**, plant, earthworm, spider and bee data from 357 grassland fields in six regions were examined. We conducted a similar analysis as in chapter 1, but we expected a smaller effect of agricultural management on communities than in arable fields. Indeed, that was the case. Instead, an additional, independent percentage of variation in species composition of plants, spiders and bees and in species richness of plants was explained by surrounding landscape.

The **Synthesis of Chapter 1 and 2** compared species richness and species composition of the arable and grassland fields that were analysed in chapters 1 and 2. Similarities and differences were discussed based on the findings of the two previous chapters.

In the investigation in **Chapter 3**, we assessed the effect of organic versus non-organic farming on species diversity of plants, earthworms, spiders and bees in 1470 habitats of 205 farms in twelve regions. Species diversity of the four taxonomic groups was on average 10% higher under organic farming. For plants and bees, this effect was clear, but for earthworms and spiders, it was not significant and inconsistent. Highest gains of organic farming were found in intensively managed arable fields (on average + 45%). However, at farm scale, where intensively managed fields as well as semi-natural habitats were considered, no significant difference between organic and non-organic farming was detected.

The study in **Chapter 4** focused on the farm scale. Plant, earthworm, spider and bee species diversity in 139 habitats of 19 farms in Stalden (Central Switzerland) was analysed. Habitats for grass, hay and silage production, as well as field margins and non-productive habitats were included. For all farms, two metrics for species diversity were evaluated: AR = Average richness, which reflects the expected species richness in a random sample taken on the farm and FU = farm uniqueness, which estimates the contribution of a farm to the total species richness under study (adapted from Wagner and Edwards, 2001). Whereas a high average

richness would benefit the fulfillment of ecological functions, the farm uniqueness indicates the value of farm regarding species conservation. In general, reducing the mechanical field operations increased average richness and a high number of low-input habitats increased farm uniqueness. To proceed in implementing measures that benefit species diversity in farmland, appropriate scientific information, such as provided by the two presented metrics, is vital. However, further steps to adequately communicate these issues are needed.

The contribution of Gisela Lüscher to the data collection, analysis and publication of the contents in this thesis was as follows:

- Organization of and contribution to data collection in the case study region Stalden (Central Switzerland) of the BioBio project
- Identification of the wild bee species from the case study region Stalden
- **Chapter 1**, data preparation, statistical analysis and main author
- **Chapter 2**, data preparation, statistical analysis and main author
- **Synthesis of Chapter 1 and 2**, data preparation, statistical analysis and author
- **Chapter 3**, data preparation and contribution to writing
- **Chapter 4**, data preparation, statistical analysis and main author

ZUSAMMENFASSUNG

Die hier vorliegende Arbeit untersuchte eine grundlegende Komponente der Biodiversität in landwirtschaftlich genutzten Flächen: Die Diversität der Arten. Dafür wurden vier taxonomische Gruppen, Pflanzen, Regenwürmer, Spinnen und Bienen, ausgewählt, die unterschiedliche Lebensweisen und Bedürfnisse haben. Diese vier taxonomischen Gruppen wurden im Rahmen des Projekts BioBio auf 205 Landwirtschaftsbetrieben in zehn europäischen und zwei afrikanischen Regionen gesammelt, bestimmt und ausgewertet. Das Ziel der Untersuchung war, Muster in den Artengesellschaften aufgrund verschiedener Bewirtschaftungssysteme zu entdecken, sowie unterschiedliche Reaktionen der vier taxonomischen Gruppen auf Bewirtschaftungsmassnahmen und landschaftliche Merkmale aufzuzeigen. Dies erfolgte in mehreren Regionen sowohl auf Habitats- wie auch auf Betriebsebene. Zuletzt wurde ein Vorschlag erarbeitet, wie Information zur Diversität der Arten auf einem Landwirtschaftsbetrieb kommuniziert und somit als Grundlage für Entscheidungen verwendet werden kann.

Für die Studie in **Kapitel 1** wurden die Artengesellschaften von Ackerbegleitflora, Regenwürmern, Spinnen und Bienen in 167 Äckern aus vier Regionen analysiert. Dafür wurden die Aspekte Abundanz, Artenreichtum und Artenzusammensetzung berücksichtigt. Mittels Variationspartitionierung schätzten wir die Anteile der Varianz in den Artengesellschaften, die von Einflussfaktoren aus drei Gruppen erklärt wurden: (i) der geographischen Lage, (ii) den Bewirtschaftungsmassnahmen und (iii) der Umgebung in einem 250 m Radius. Während die geographische Lage allgemein den stärksten Einfluss auf alle Artengesellschaften ausübte, war auch der Einfluss der Bewirtschaftungsmassnahmen auf die Ackerbegleitflora, die Spinnen und die Bienen sehr deutlich. Umgebungsmerkmale

hingegen zeigten weniger Zusammenhänge mit den Artengesellschaften. Generell förderten der Verzicht auf mineralischen Stickstoff und Pestizide die Abundanz und den Artenreichtum, wobei die vier taxonomischen Gruppen jedoch je individuell auf Bewirtschaftungsmassnahmen und Umgebungsmerkmale reagierten.

Für die Studie in **Kapitel 2** standen Daten zu Pflanzen-, Regenwurm-, Spinnen- und Bienengesellschaften von 357 produktiven Graslandflächen in sechs Regionen zur Verfügung. Wir führten eine ähnliche Analyse wie für die Ackerflächen in Kapitel 1 durch, erwarteten jedoch einen geringeren Einfluss von Bewirtschaftungsmassnahmen auf die Artengesellschaften als in den Äckern. Dies war der Fall. Dafür wurde zusätzlich ein signifikanter Anteil der Varianz in der Artenzusammensetzung von Pflanzen, Spinnen und Bienen und dem Artenreichtum von Pflanzen durch die Umgebung erklärt.

In der **Synthese von Kapitel 1 und 2** wurden die Äcker und Graslandflächen aus den Kapiteln 1 und 2 hinsichtlich ihres Artenreichtums und ihrer Artenzusammensetzung verglichen. Gemeinsamkeiten und Unterschiede wurden mit Hilfe der gewonnen Erkenntnisse aus den ersten beiden Kapiteln diskutiert.

Die Untersuchung in **Kapitel 3** schätzte den Einfluss von biologischer und nicht-biologischer Bewirtschaftung auf die Artenvielfalt von Pflanzen, Regenwürmern, Spinnen und Bienen in 1470 Habitaten von 205 Betrieben in 12 Regionen. Die biologische Bewirtschaftung führte zu einer Erhöhung der Artenvielfalt um durchschnittlich 10% für die vier untersuchten taxonomischen Gruppen. Dieser Effekt war deutlich für Pflanzen und Bienen aber nur marginal und uneinheitlich für Regenwürmer und Spinnen. Der grösste Gewinn für die Artenvielfalt aufgrund von biologischer Bewirtschaftung war auf intensiv genutzten Äckern zu finden (durchschnittlich + 45%). Ein Vergleich auf Betriebsebene hingegen, wo sowohl

intensiv genutzte als auch naturnahe Habitate mit einflossen, ergab keinen signifikanten Unterschied zwischen biologischer und nicht-biologischer Bewirtschaftung.

Die Studie in **Kapitel 4** weitete ebenfalls den Blick von der Habitats- auf die Betriebsebene. Die Artenvielfalt von Pflanzen, Regenwürmern, Spinnen und Bienen in 139 Habitaten von 19 Betrieben in der Zentralschweiz wurde beurteilt. Dabei wurden sowohl Habitate berücksichtigt, die für die Produktion von Gras, Heu und Silage bewirtschaftet wurden, wie auch Randbereiche und naturnahe Habitate, die zur Betriebsfläche gehörten. Alle Betriebe wurden anhand von zwei Messgrössen bewertet: erstens anhand des Artenreichtums auf einer durchschnittlichen Untersuchungsfläche (AR = Average richness) und zweitens anhand der sogenannten Betriebseinzigartigkeit für hohen Artenreichtum und das Vorkommen von seltenen Arten (FU = Farm uniqueness, adaptiert von Wagner und Edwards 2001). Während ein hoher durchschnittlicher Artenreichtum als generell günstig für die Ausführung von ökologischen Funktionen betrachtet werden kann, weist die Betriebseinzigartigkeit auf die Bedeutung des Betriebs für die Erhaltung der Artenvielfalt bei. Allgemein war eine Reduktion der mechanisierten Arbeitsschritte günstig für den durchschnittlichen Artenreichtum, und eine erhöhte Anzahl extensiv bewirtschafteter Habitate förderte die Betriebseinzigartigkeit. Damit wirkungsvolle Massnahmen zur Förderung der Artenvielfalt auf Landwirtschaftsbetrieben angewendet werden, ist verlässliche, wissenschaftliche Information notwendig. Messgrössen, so wie die beiden hier vorgestellten, sind dafür hilfreich. Weiter ist es wichtig, dass diese Information sorgfältig und auf angepasste Art und Weise kommuniziert wird.

CHAPTER 1

Responses of Plants, Earthworms, Spiders and Bees to Geographic Location, Agricultural Management and Surrounding Landscape in European Arable Fields

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Abstract

Farmland species provide key ecological services that support agricultural production, but are under threat from agricultural intensification and mechanization. In order to design effective measures to mitigate agricultural impact, simultaneous investigations of different taxonomic groups across several regions are required. Therefore, four contrasting taxonomic groups were investigated: plants, earthworms, spiders and bees (wild bees and bumblebees), which represent different trophic levels and provide different ecological services. To better

understand underlying patterns, three community measurements for each taxonomic group were considered: abundance, species richness and species composition. In four European regions, ten potential environmental drivers of the four taxonomic groups were tested and assigned to three groups of drivers: geographic location (farm, region), agricultural management (crop type, mineral nitrogen input, organic nitrogen input, mechanical field operations and pesticide applications) and surrounding landscape in a 250 m buffer zone (diversity of habitats in the surroundings, proportion of arable fields and proportion of non-productive, non-woody habitats). First, the variation in abundance, species richness and species composition from 167 arable sites was partitioned to compare the relative contribution of the three groups of drivers (geographic location, agricultural management and surrounding landscape). Second, generalized linear mixed-effects models were applied to estimate the effect of the individual explanatory variables on abundance and species richness. Our analysis showed a dominant effect of geographic location in all four taxonomic groups and a strong influence of agricultural management on plants, spiders and bees. The effect of the surrounding landscape was of minor importance and inconsistent in our data. We conclude that in European arable fields, the avoidance of mineral nitrogen and pesticides is beneficial for biodiversity, and that species protection measures should take into account regional characteristics and the community structure of the investigated taxonomic groups.

Keywords

Abundance, Species richness, Species composition, Partitioning of variation, BioBio

1. Introduction

Although the production of agricultural goods depends, in part, on ecological services provided by farmland species, human activities often impair biodiversity (Hector and Bagchi, 2007; Sachs et al., 2009). Intensive agricultural management may deplete beneficial species

that contribute to, for example, soil fertility, decomposition, biological control or pollination (Costanza et al., 1997). Such species are particularly threatened in arable fields, which face regular disturbances due to intensive management for optimized resource use and crop protection (Matson et al., 1997; Robinson and Sutherland, 2002).

Agri-environment schemes are implemented to mitigate the pressure on biodiversity and to promote farmland species. While they have frequently been shown to benefit farmland species, the magnitude of the effects has varied among studies (Batáry et al., 2010; Gibson et al., 2007). These ambiguous results have been attributed to differences in taxonomic groups, study regions and scales of investigation (Bengtsson et al., 2005). In addition, several studies have concluded that more detailed insights into the drivers of farmland species could be achieved if both landscape characteristics and management practices were considered (Batáry et al., 2011; Chaplin-Kramer and Kremen, 2012; Concepción et al., 2012a; Schweiger et al., 2005; Tscharntke et al., 2005).

Many studies of farmland species have been limited to only one or a few popular taxonomic groups. However, the effects of agricultural management and of landscape characteristics on a particular taxonomic group are likely to depend on its specific resource needs, such as food or habitat requirements (Aviron et al., 2009; Báldi et al., 2013; Kleijn et al., 2006; Schuldt and Assmann, 2010). In order to promote agricultural practices with targeted benefits for biodiversity, it is therefore important to evaluate their impacts on multiple taxonomic groups. Further, it may also be important to evaluate multiple community measurements such as abundance, species richness and species composition, as these may have different specific effects on ecological services (Isbell et al., 2011) and different sensitivities to the agricultural environmental drivers (Jeanneret et al., 2003; Worthen, 1996).

Here, we investigated plant, earthworm, spider and bee (wild bee and bumblebee) communities in 167 arable fields across four European regions. The four taxonomic groups were chosen because they have different habitat and food requirements, provide a range of ecological services and occupy different trophic levels. Plants, as primary producers and sessile organisms, depend on light, water and nutrients available on site. Plant abundance and species richness in arable fields have been found to decrease due to management intensity (mineral nitrogen input, pesticide applications) in numerous studies, e.g. Hyvönen and Salonen (2002) and Rassam et al. (2011). Further, plant diversity, mainly in field edges, is enriched by a higher amount of semi-natural habitats in the surrounding landscape (Concepción et al., 2012b; Kovács-Hostyánszki et al., 2011). Earthworms, as detritivores and soil organisms, contribute to soil fertility. They are positively affected by the application of solid manure, mulches and reduced tillage (Chan, 2001). Spiders are a widely distributed and highly abundant group of predators for which several studies have emphasized the significance of (perennial) vegetation structure (e.g. Gibson et al., 1992 or Schmidt and Tscharntke, 2005). Wild bees and bumblebees act as pollinators and are highly mobile. They depend on a continuous pollen and nectar supply in the wider landscape and on appropriate nesting sites (e.g. Kremen et al., 2007).

We tested how plant, earthworm, spider and bee communities in the same arable fields responded to explanatory variables representing geographic location, agricultural management and surrounding landscape. For all communities, abundance, species richness and species composition were considered to gain more information on community patterns than one measurement alone could provide. The four taxonomic groups were expected to differ in their responses, and that these differences were reflected in existing or missing correlations among the taxonomic groups. However, because arable fields are predominantly shaped by agricultural practices for the purpose of crop production, we hypothesized that management

variables have a significant effect on the four taxonomic groups, independent of geographic location and surrounding landscape.

2. Materials and Methods

2.1. Study Sites

Data collection was part of the EU-FP7 project BioBio, which investigated and proposed a set of biodiversity indicators applicable for European farmland monitoring (Herzog et al., 2012). This study investigated 167 arable fields from four European regions: Marchfeld (Austria), Southern Bavaria (Germany), Gascony (France) and Homokhátság (Hungary).

Each region was an environmentally homogeneous area, representing either typical arable cropping or a combination of arable cropping and grassland-based livestock farming (Table 1). In each region of approximately 1000 km^2, between 14 and 16 study farms, half of them organic and half non-organic, were randomly selected. The whole area of these farms was mapped by classifying different habitat types according to primary life forms, environment and management (Bunce et al., 2008). One of four crop categories was assigned to each arable field: winter cereals, spring cereals, forage crops (e.g. lucerne, grass-clover) and others (e.g. oilseed rape). For each available crop category per farm, one field was randomly selected for species sampling.

Table 1: Geographic coordinates, environmental and agricultural characteristics of the study regions.

Region	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Country	Austria	Germany	France	Hungary
Latitude (°)	48.3	48.4	43.4	46.7
Longitude (°)	16.7	11.3	0.8	19.6
Altitude (m asl)	140-180	350-500	197-373	93-168
Climate	Pannonian	Continental	Sub-Mediter.	Pannonian
Rainfall (mm)	560	800	680	550
Mean annual temp. (°C)	9.5	8.5	13	10.4
Soil	Deep fertile chernozem	Silt and silt loam	Clay-limestone	Sandy
Production type	Arable crops	Mixed	Arable crops	Mixed
# Arable fields (in # farms)	56 (16)	49 (16)	39 (15)	23 (14)

2.2. Species Sampling

In each randomly selected arable field, species of the four taxonomic groups were sampled from spring to early autumn in 2010 according to standardized protocols (Dennis et al., 2012). Sample locations were chosen such that edge effects were avoided. Plant surveys were conducted once, in a plot of 10 m × 10 m. All species were recorded and their respective cover estimated. Cultivated crop species were excluded from the analysis except the forage crops. Earthworms were collected at three random locations per field, at one time. A solution of allyl isothiocyanate (0.1 g/l) was poured into a metal frame of 30 cm × 30 cm in order to encourage earthworms to move to the surface. Subsequently, earthworms were collected by hand from a 20 cm deep earth core. Identification and counting of earthworms species was conducted in the lab. Non-clitellates (juveniles and subadults) were excluded from the analysis. Spiders were sucked from the surface at three dates during the season from within five randomly located circular areas of 35.7 cm diameter per field using a modified leaf blower. The samples were frozen and adults were identified in the lab. Wild bee and bumblebee species were sampled during good weather conditions, i.e. during periods of sunshine when it was not too windy and the temperature was higher than 15 °C. Bees were

sampled on three dates with a handheld net along a 100 m × 2 m transect traversing the plant survey plot for 15 min, except in the Marchfeld region, where bees were sampled only twice due to bad weather. Honeybees (*Apis mellifera)* were excluded from the analysis.

2.3. Response Variables

Three community measurements were calculated as response variables: abundance, species richness and species composition. Abundance was expressed as the percentage cover for plants and the total number of individuals per field for earthworms, spiders and bees. Species richness was calculated as the total number of species in a field. Species composition was quantified as the species list for each taxonomic group, accounting for abundance per field.

2.4. Explanatory Variables

Potential environmental drivers were divided into three groups of variables for (1) geographic location, (2) agricultural management and (3) surrounding landscape.

Geographic location: Two variables, farm (fields belonged to 61 farms) nested within region (four groups), were assigned to each investigated field as descriptors of general geographic conditions. The variable farm accounted for general features of the farm (e.g. location, overall farming intensity or the crop rotation system). The variable region incorporated characteristics such as climatic conditions, soil properties and large-scale landscape features (e.g. exclusively arable cropping or mixed farming, occurrence of forest or water bodies) as well as historic processes of landscape changes.

Agricultural management: For all investigated fields, management practices in 2010 were recorded in structured interviews with farmers. Since a large number of agricultural management variables were partially correlated, we pre-selected the five that were only weakly correlated using correlation coefficients and variance inflation factors, according to Borcard et al. (2011). The final group of agricultural management variables consisted of: crop

type, amount of mineral nitrogen (N) fertilizer applied, amount of organic nitrogen (N) fertilizer applied, number of mechanical field operations and number of synthetic and natural pesticide applications. For the analysis, we regrouped the original division of four crop types into six crop types according to sowing time and management practices (winter cereals, spring cereals, Fabaceae, forage plants, maize/sunflower and miscellaneous crops such as oilseed rape, potato or sugar beet). Winter cereals were the most abundant crop type, followed by forage plants and maize/sunflower (Table 2). In general, fields with Fabaceae and forage plants were less intensively managed regarding N input and pesticide applications than fields sown with miscellaneous crops and maize/sunflower. In order to detect the specific drivers (e.g. mineral N input or pesticide applications) of community structures, organic and non-organic fields were not separated in the analysis. The N input and the mechanical field operations were remarkably high in Southern Bavaria (Table 2). Pesticides were applied on 58 of the 167 fields, 34 fields were treated more than once. Pesticides were mainly herbicides, fungicides and rarely insecticides, retardants or molluscicides.

Surrounding landscape: Based on aerial photographs, the landscape composition was recorded in a buffer zone around each investigated field. The radius of the buffer zone was set at 250 m as a compromise for the four contrasting taxonomic groups (Gaba et al., 2010; Schmidt et al., 2008; Zurbuchen et al., 2010). Initially, the buffer zone was subdivided into nine habitat categories, and the estimates of percentage of habitat cover were used to calculate a Shannon diversity index H (based on the natural logarithms) of the surrounding habitats for each field. Then, the percentage cover of four aggregated habitat groups was calculated: (a) arable fields, (b) grasslands, (c) woody habitats (forest, scrub and woody crops) and (d) non-productive, non-woody habitats (urban area, sparsely vegetated ground, aquatic habitats, emergent hydrophytes or helophytes). Similar to agricultural management variables, the number of surrounding landscape variables was reduced to three: diversity of habitats in the

surroundings, proportion of arable fields and proportion of non-productive, non-woody habitats (Table 2).

Table 2: Characteristics of the investigated arable fields: mean ± standard error of numeric variables and levels of the categorical variable crop type in each study region (in order of frequency).

Region		Marchfeld	Southern Bavaria	Gascony	Homokhátság
Agricultural management	Mineral N input (kg/ha)	40 ± 7	52 ± 9	34 ± 8	2 ± 2
	Organic N input (kg/ha)	7 ± 3	56 ± 6	16 ± 5	53 ± 10
	Field operations	6 ± 0.3	12 ± 1	5 ± 0.4	3 ± 0.2
	Pesticide applications	1 ± 0.2	0.8 ± 0.2	0.9 ± 0.2	0
	Crop types	WiC, For, Fab, M/S, Mis, SpC	WiC, For, M/S, Fab, Mis	WiC, S, Fab, For, SpC	For, WiC, M/S
Surrounding landscape	H[a] of surrounding habitats	0.2 ± 0.04	0.9 ± 0.04	0.7 ± 0.05	0.8 ± 0.05
	Arable fields (%)	90.2 ± 2.2	63.7 ± 2.3	74.9 ± 2.6	43.5 ± 3.9
	Non-productive, non-woody habitats (%)	3.9 ± 1.5	6 ± 0.8	2.4 ± 0.8	5.7 ± 2.4

Abbreviations for the crop types: WiC, winter cereals; SpC, spring cereals; For, forage crops; Fab, Fabaceae; M/S, maize/sunflower; Mis, miscellaneous crops.
[a] H = Shannon diversity index

2.5. Data Analysis

The relative roles of the three groups of explanatory variables were calculated: geographic location, agricultural management and surrounding landscape on the three response variables per taxonomic group.

Partitioning of variation was used to quantify the variation in abundance, species richness and species composition due to the three groups of explanatory variables (Borcard et al., 2011). The three groups were not fully independent of each other; therefore, some variation was explained jointly by two or by all three groups. The percentages of variation due to a single group of explanatory variables or a combination of groups were reflected in the adjusted R^2, which were calculated by partial redundancy analysis (RDA). Significance of percentages allocated to single groups was assessed based on 999 permutations (Legendre and Legendre,

2012). Because partitioning of variation relies on linear regressions, the univariate response variables, abundance and species richness, were log-transformed after adding a constant c = 0.5 (½ of the smallest non-zero value). Species composition data, as multivariate response variables, were Hellinger transformed (Legendre and Gallagher, 2001).

Generalized linear mixed-effects models were used to analyse effects of the individual explanatory variables on abundance and species richness. Since the response variables were over-dispersed with respect to a Poisson model, we assumed that they followed a negative binomial distribution. Bee data contained more than 60% zeros. Therefore, we applied models that accounted for zero-inflation. Agricultural management and surrounding landscape variables were treated as fixed effects, and interactions among fixed effects were included when significant. Region was included as a random intercept in all models. If, as an additional random intercept, farm improved the fit of the model significantly, it was included, also. The influence of individual crop types was tested against the most abundant crop type, the winter cereals. Models were reduced based on the AIC (Akaike information criterion) corrected for small samples (Burnham and Anderson, 2002). The significance of the reduced models was assessed with sequential likelihood-ratio tests.

Correlations in abundance, species richness and species composition among the four taxonomic groups, were calculated separately for all four regions based on untransformed species data. For abundance and species richness, Spearman's rank correlation coefficients were calculated in order to account for the non-normal distribution of the data. Procrustes rotation was used to test for correlations among the species compositions of the four taxonomic groups (Legendre and Legendre, 2012).

All analyses were performed in R 2.15.3 (R Development Core Team, 2012) using packages vegan 2.0-6, vennerable, plotrix, glmmADMB 0.7.3, AICcmodavg 1.27 and lmtest.

3. Results

In the entire set of 167 arable fields, 2,565 adult earthworm individuals, 1,967 adult spider individuals and 343 bee individuals were found. We identified 292 plant species, 19 earthworm species, 158 spider species and 72 wild bee and bumblebee species. The complete species lists and the number of fields in which they occurred are provided in Appendices S2, S3, S4 and S5 in Supplementary Material. In the Gascony region, the highest number of species was recorded for all four taxonomic groups (Fig. 1). For plants, 5% of all species occurred in all four regions and covered 30% of the area investigated (167 x 100 m^2). Five common species in all four regions with a high overall abundance were *Chenopodium album*, *Cirsium arvense*, *Convolvulus arvensis*, *Lolium perenne* and *Medicago sativa*. For earthworms, the most common species were *Allolobophora caliginosa* and *A. rosea*, which accounted for 55% of all earthworm individuals. For spiders, 4% of all species were recorded in all regions, and these made up 34% of the total spider abundance. The spider species *Erigone dentipalpis*, *Meioneta rurestris* and *Pachygnatha degeeri* were highly abundant and are among others listed by Schmidt and Tscharntke (2005) as so called agrobionts, i.e. species that "invariably dominate spider communities in crop fields over large parts of Europe." One bumblebee species, *Bombus terrestris*, was common in all regions, accounting for 13% of all bee individuals.

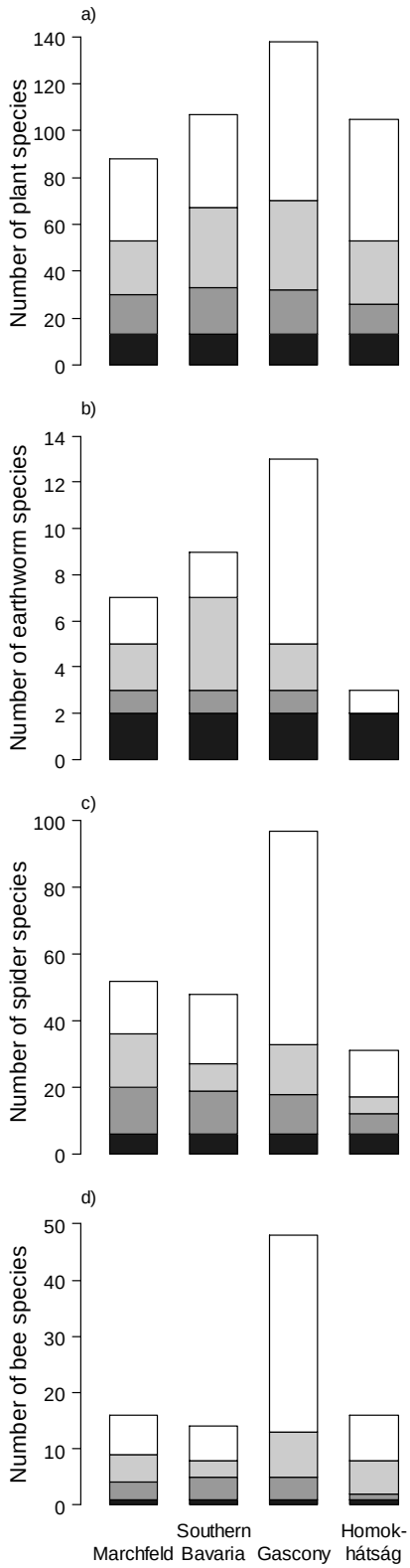

Fig. 1: Total number of (a) plant, (b) earthworm, (c) spider and (d) bee species in each region. Grey shading indicates the number of species occurring: in all four regions (black), in three regions (dark grey), in two regions (light grey), exclusively in the corresponding region (white).

3.1. Plants

Variation in plant abundance of non-crop species was primarily explained by agricultural management (22%) and geographic location (18%), but not by surrounding landscape (Fig. 2). Variation in plant species richness was mainly explained by combinations of geographic location, agricultural management and surrounding landscape. None of the groups of explanatory variables explained a significant percentage of the variation independently of other variables. The variation in plant species composition was equally well explained by geographic location (10%) and agricultural management (10%), but not by surrounding landscape.

The generalized linear mixed-effects model revealed a negative effect of mineral N input and a positive effect of organic N input on plant abundance (Table 3). The interaction of organic N input and the proportion of arable fields in the surroundings was negative. This indicated that the positive effect of the combination of the both variables was weaker than the sum of the two variables. Crop type was also important: plant abundance in winter cereal fields was significantly lower than in forage fields and was significantly higher than in maize/sunflower fields. Mineral N input and pesticide applications had a negative effect on plant species richness (Table 4). Further, the interactions of mineral N input and pesticide applications and of mineral N input and mechanical fields operations were significantly positive. Thus, the detrimental effect of the two involved variables in combination was weaker than the sum of them. Plant species richness was significantly higher in winter cereal fields than in maize/sunflower fields, and the diversity of habitats in the surroundings had a positive effect.

3.2. Earthworms

Variation in earthworm abundance, species richness and species composition was predominantly explained by geographic location at percentages of 55%, 47% and 21%,

respectively (Fig. 2). Neither agricultural management nor surrounding landscape explained a significant percentage of variation in earthworm communities independently.

Also in the mixed models, none of the agricultural management and surrounding landscape variables had a significant effect on earthworm abundance and species richness (Table 3 and 4).

3.3. Spiders

Variation in spider abundance, species richness and species composition was similarly significantly explained by geographic location (11%, 12% and 10%, respectively) and agricultural management (9%, 6% and 6%, respectively), but not by surrounding landscape (Fig. 2).

The mixed model indicated a positive effect of organic N input on spider abundance and species richness (Table 3 and 4). Furthermore, spider abundance and species richness were significantly higher in forage fields than in winter cereal fields, and maize/sunflower fields harboured significantly fewer spider species than winter cereal fields.

3.4. Bees

Variation in bee abundance and species richness was largely explained by geographic location (22% and 15%, respectively) but not by agricultural management or surrounding landscape (Fig. 2). Bee species composition was highly variable and none of the groups of explanatory variables tested had a significant effect.

The mixed models showed a negative effect of pesticide applications on bee abundance and species richness (Table 3 and 4). Mineral N input affected bee species richness negatively. Both, abundance and species richness, were higher in forage fields than in winter cereal fields. Furthermore, habitat diversity as well as the proportion of arable fields and the proportion of non-productive, non-woody habitats in the surroundings decreased bee abundance and species

richness. The interaction of habitat diversity and the proportion of non-productive, non-woody habitats was positive for bee abundance and species richness and the interaction of the proportion of arable fields and the proportion of non-productive, non-woody habitats also for species richness. This indicated that the detrimental effect of the two involved variables in combination was weaker than the sum of them.

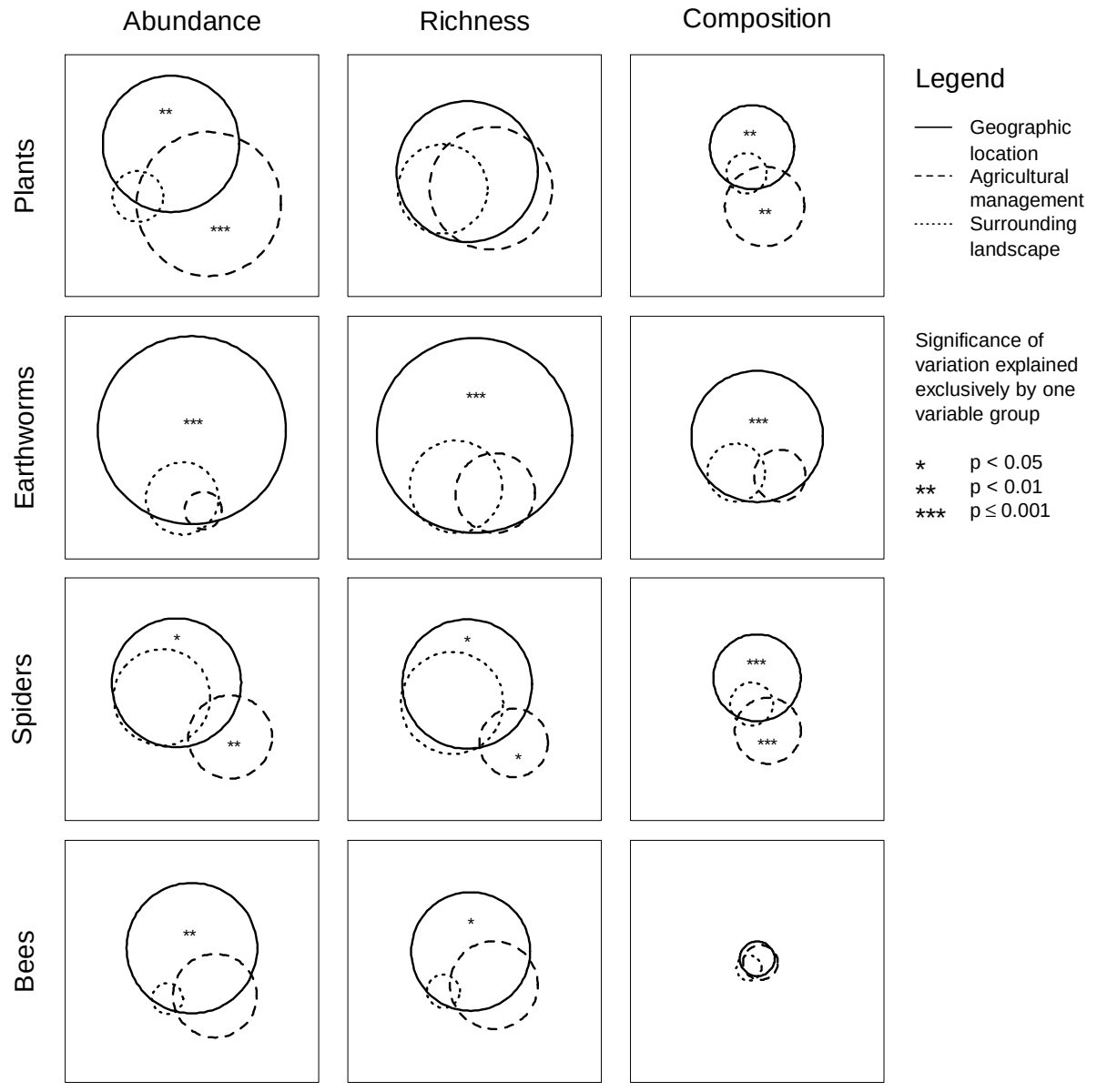

Fig. 2: Partition of variation in abundance, species richness and species composition of plants, earthworms, spiders and bees explained by geographic location, agricultural management and surrounding landscape derived from partial redundancy analysis. The area of the circles is proportional to the percentage of variation explained by the respective group of explanatory variables. Each box accounts for the total variation (100 %), i.e. the area outside of the circles represents the amount of unexplained variation.

Table 3:Effects of geographic location, agricultural management and surrounding landscape variables on the abundance of plants, earthworms, spiders and bees estimated using negative binomial generalized linear mixed-effects models.

	Plants			**Earthworms**			**Spiders**			**Bees**		
Fixed effects	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*
Winter cereals (Intercept)	**2.96**	**0.48**	**<0.001**	**2.25**	**0.45**	**<0.001**	**1.92**	**0.30**	**<0.001**	**5.45**	**1.41**	**<0.001**
Spring cereals	-0.24	0.26	0.35				-0.05	0.26	0.85	-0.96	0.62	0.12
Fabaceae	0.18	0.23	0.44				-0.33	0.23	0.16	0.34	0.29	0.24
Forage crops	**1.39**	**0.17**	**<0.001**				**0.83**	**0.18**	**<0.001**	**0.83**	**0.24**	**<0.001**
Maize/sunflower	**-0.50**	**0.19**	**<0.01**				-0.31	0.20	0.13	0.23	0.26	0.38
Miscellaneous	-0.55	0.35	0.12				0.21	0.32	0.52	-	-	-
Mineral N input (kg/ha)	**-0.007**	**0.002**	**<0.001**									
Organic N input (kg/ha)	**0.02**	**0.01**	**<0.01**				**0.006**	**0.002**	**<0.01**			
Pesticide applications										**-0.67**	**0.17**	**<0.001**
H[a] of surrounding habitats										**-3.21**	**0.70**	**<0.001**
Arable fields in the surroundings (%)	0.005	0.005	0.29							**-0.05**	**0.01**	**<0.001**
Non-productive, non-woody habitats in the surroundings (%)										**-0.08**	**0.04**	**<0.05**
H[a] of sur. hab. * N-p, n-w. hab.										**0.12**	**0.04**	**<0.01**
Organic N input * arable fields	**-0.0002**	**0.0001**	**<0.01**									
Random effects	SD			SD			SD			SD		
Region (Intercept)	0.60			0.88			0.54			1.29		
Farm	0.35			0.52						0.46		
		SE			SE			SE			SE	
Negative binomial dispersion parameter	2.07	0.30		2.20	0.39		1.65	0.22		24.04	34.48	
Zero-inflation										0.30	0.06	

Bee abundance data were analysed with a model accounting for zero-inflation. *P*-values were calculated from likelihood-ratio tests. Significant fixed effects are marked in bold.

[a] H = Shannon diversity index

Table 4: Effects of geographic location, agricultural management and surrounding landscape variables on species richness of plants, earthworms, spiders and bees estimated using negative binomial generalized linear mixed-effects models.

	Plants			**Earthworms**			**Spiders**			**Bees**		
Fixed effects	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*
Winter cereals (Intercept)	**2.48**	**0.18**	**<0.001**	**0.79**	**0.31**	**<0.05**	**1.34**	**0.28**	**<0.001**	**3.61**	**1.26**	**<0.01**
Spring cereals	0.23	0.15	0.12				-0.04	0.19	0.84	-0.55	0.58	0.34
Fabaceae	-0.23	0.13	0.08				-0.18	0.17	0.30	0.32	0.28	0.26
Forage crops	-0.10	0.11	0.33				**0.39**	**0.13**	**<0.01**	**0.63**	**0.24**	**<0.01**
Maize/sunflower	**-0.23**	**0.12**	**<0.05**				**-0.42**	**0.15**	**<0.01**	0.04	0.27	0.87
Miscellaneous	-0.30	0.26	0.24				0.01	0.24	0.95	-	-	-
Mineral N input (kg/ha)	**-0.01**	**0.00**	**<0.001**							**-0.007**	**0.004**	**<0.05**
Organic N input (kg/ha)							**0.005**	**0.001**	**<0.001**			
Field operations	-0.01	0.01	0.51									
Pesticide applications	**-0.16**	**0.07**	**<0.05**							**-0.37**	**0.17**	**<0.05**
Mineral N input * field op.	**0.0006**	**0.0001**	**<0.001**									
Mineral N input * pesticide appl.	**0.002**	**0.001**	**<0.05**									
H[a] of surrounding habitats	**0.30**	**0.15**	**<0.05**							**-1.96**	**0.63**	**<0.01**
Arable fields in the surroundings (%)										**-0.03**	**0.01**	**<0.01**
Non-productive, non-woody habitats in the surroundings (%)										**-0.23**	**0.10**	**<0.05**
H[a] of sur. hab. * N-p, n-w. hab.										**0.16**	**0.06**	**<0.01**
Arable fields * N-p, n-w. hab.										**0.002**	**0.001**	**<0.05**
Random effects	SD			SD			SD			SD		
Region (Intercept)	0.24			0.60			0.50			0.94		
		SE			SE			SE			SE	
Negative binomial dispersion parameter	8.57	1.98		403.43	0.57		5.88	1.53		403.43	1.97	
Zero-inflation										0.26	0.07	

Species richness of bees was analysed with a model accounting for zero-inflation. *P*-values were calculated from likelihood-ratio tests. Significant fixed effects are marked in bold.

[a] H = Shannon diversity index

3.5. Correlations

Correlations between the four taxonomic groups differed between regions (Table 5). If significant, all correlations within abundances and species richness values were positive except one significantly negative correlation between plant and earthworm species richness in the Homokhátság region. Significant correlations were most frequently found between plants and bees. A few positive correlations were found between plants and spiders, between earthworms and spiders and between spiders and bees.

Table 5: Range of pairwise Spearman's rank correlations (abundance and species richness) and Procrustes rotation parameter (species composition) between the four taxonomic groups in the four case study regions.

	Abundance		Richness		Composition	
	Spearman's correlation coefficient	Regions where significant	Spearman's correlation coefficient	Regions where significant	Correlation in a symmetric Pro-crustes rotation	Regions where significant
Plants vs. earthworms	-0.22 – 0.19	-	-0.42 – 0.18	H (-)	0.28 – 0.39	H
Plants vs. spiders	0.14 – 0.51	D (+)	-0.01 – 0.47	F (+)	0.36 – 0.53	A, D
Plants vs. bees	0.19 – 0.55	A, D, F (all +)	0.04 – 0.37	A, D (all +)	0.40 – 0.61	A, F
Earthworms vs. spiders	0.17 – 0.34	A (+)	0.22 – 0.24	-	0.35 – 0.39	A, D
Earthworms vs. bees	-0.06 – 0.17	-	-0.20 – 0.18	-	0.23 – 0.39	-
Spiders vs. bees	-0.10 – 0.43	D, H (all +)	-0.20 – 0.41	D (+)	0.28 – 0.46	-

Regions where coefficients were significant are given as A = Marchfeld, D = Southern Bavaria, F = Gascony, H = Homokhátság.

4. Discussion

4.1. Abundance, Species Richness and Species Composition

In plant communities, the patterns of explained variation differed strongly among abundance, species richness and species composition. For example, plant abundance responded to crop type far more than plant species richness responded. This can be explained by the fact that the crop type governed the dominance of a small number of very common weed species, in

particular *Avena fatua* and *C. arvense*, as well as the forage crops *M. sativa*, *Trifolium pratense* and *Lolium multiflorum*, but affected the presence or the absence of all other species to a lesser degree. A similarly low impact of crop type on plant species richness was also reported by Fried et al. (2008). Nevertheless, a high percentage of variation in plant species richness was jointly explained by geographic location, agricultural management and surrounding landscape, indicating that explanatory variables had combined effects. For example, plants species richness increased with a higher diversity of habitats in the surroundings and a lower mineral N input.

In the faunistic communities, the patterns of explained variation were relatively similar for abundance, species richness and species composition. One exception was the variation in bee species composition that appeared to be largely unrelated to the investigated explanatory variables. A reason for this exception might be that the few, non-empty bee samples were highly divergent and therefore, no structure in bee assemblages was detected. Generally, if explanatory variables explained variation in species composition of the faunistic groups, it was reflected in abundance and species richness. This is in contrast to findings of Báldi et al. (2013) which showed that species compositions of several taxa, including spiders and bees, responded to environmental drivers in grassland fields but their species richnesses did not. We hypothesize that species communities in arable fields are subject to greater and more frequent fluctuations, and beneficial conditions might be too short to establish intensive interactions between species. Therefore, we would expect such interactions to result in relatively stable species compositions, which would respond differently to environmental factors considering species richness or species composition.

Whereas it was obvious that the consideration of abundance, species richness and species composition provided complementary information for plants, the three community

measurements for the faunistic groups provided similar results. The similarity among the community measurements is an important result, because it indicates that species community structures might depend on species mobility and disturbance frequencies in habitats.

4.2. Responses of Taxonomic Groups

Plant abundance and species richness were diminished by management intensity, in line with Hyvönen and Salonen (2002) and Rassam et al. (2011). Fields with higher mineral N input had lower plant abundance and species richness than fields with additional or exclusive organic N input or fields that were not fertilized. The positive effect of organic N input should not be interpreted as a univariate relationship but as an additive effect. Its negative interaction with the proportion of arable fields in the surrounding landscape indicated that plant abundance in fields located in a homogeneous landscape of arable cropping benefited less from organic fertilization. Pesticide applications were detrimental for plant species richness. Crop type also affected plant communities probably due to crop-specific management practices and direct competition for water, nutrients and light. Similar to Pysek et al. (2005), maize/sunflower fields had lower plant abundance and species richness than cereal fields. Furthermore, plant species richness increased with the diversity of surrounding habitats, in accordance with Gabriel et al. (2005) who found higher plant species richness of arable fields in structurally more complex landscapes. Contrastingly, Bohan and Haughton (2012) and Marshall (2009) found no effect of margin strips or landscape context on weed diversity in the centre of arable fields, but did report a small effect in field edges. We assume that our result was related to a comparatively low management intensity (e.g. in the Homokhátság region), in which species with wind-dispersed seeds were abundant and succeeded to germinate within fields (compare also Concepción et al., 2012b and Tscharntke et al., 2005).

Earthworms rely on habitat and food resources at a local scale due to their restricted mobility. Not surprisingly, an effect of the surrounding landscape was lacking. However, in contrast to our expectations, we did not find a significant effect of management variables in our data. Generally, earthworms are considered vulnerable to management practices that lead to mechanical damage, increased susceptibility to predation (e.g. after cultivation), loss of an insulating layer of vegetation and a decreased food supply (Edwards and Bohlen, 1996). Indeed, abundant literature highlights the detrimental effect of inversion tillage on earthworms (e.g. Paoletti et al., 2010). The absence of significant effects in our study might be due to the relatively coarse description of management practices. In addition, the two most abundant earthworm species (the endogeic *A. caliginosa* and *A. rosea*), which accounted for more than half of all earthworm individuals, are known to be rather insensitive to agricultural management (Paoletti, 1999a).

Spider communities were found to be closely related to vegetation structure, as this provides specific microclimatic conditions, shelter and food resources (Gibson et al., 1992). Crop type also had a major effect on spider communities. The highest spider abundance and species richness were found in forage crops. Furthermore, high spider abundance and species richness under organic N input might be caused by a positive influence of organic fertilizer on epigeal arthropods, which contributed to the food supply of spiders, as mentioned in Purvis and Curry (1984). In agreement with Batáry et al. (2008), the surrounding landscape had no effect on spider abundance, which could be due to the restricted spatial scale under investigation, because landscape factors measured over larger distances have been observed to significantly affect spiders (Drapela et al., 2008; Schmidt et al., 2008).

In our study, the direct link between plant and bee species communities was evident because the same management variables, mineral N input and pesticide applications, affected

abundance and/or richness of both taxonomic groups negatively in accordance with Kremen et al. (2007) and Goulson et al. (2008). As most of the pesticides were herbicides, an indirect effect on bees via plants was suggested. However, very likely direct impacts of insecticides intensified this effect (Brittain et al., 2010; Whitehorn et al., 2012). All tested surrounding landscape variables had a negative effect on bee abundance and species richness. The negative effect of the proportion of arable fields was in line with Holzschuh et al. (2010) who found more bees in landscapes with high proportions of non-crop habitats. Surprisingly, bee abundance also decreased with a higher diversity of surrounding habitats. Steffan-Dewenter (2003) discussed this issue and noted the importance of specific habitat types in the surroundings, an aspect later studied by Carré et al. (2009), who found a decrease in bee abundance with a higher amount of surrounding forest patches, which could act as barriers. In our case, diversity of surrounding habitats was correlated with the area of woody elements in the surroundings, which suggests a similar underlying pattern.

Identical drivers acting on the four taxonomic groups were expected to result in positive correlations between the different groups. The highest agreement among drivers occurred between plant and bee communities (crop type, mineral N input and pesticide applications) and was indeed reflected in several correlations between these two groups. Correlations between plants and spiders and between spiders and bees were weak and primarily due to crop type. Correlations between plant and earthworm species richness occurred in the Homokhátság region. Interestingly, earthworm species composition was significantly correlated to spider species composition in the Marchfeld region and in Southern Bavaria, and earthworm abundance was positively correlated to spider abundance in the Marchfeld region. One reason could be that both, earthworms and spiders, were affected by the structure of the soil surface, especially soil cover by plant litter. Litter provided food resources for

earthworms and for other detritivores involved in decomposition, which might then be hunted by spiders (Purvis and Curry, 1984).

4.3. Group-specific Explanatory Power of Agricultural Management

Since arable fields are highly disturbed habitats, a direct effect of agricultural management on plant, earthworm, spider and bee communities in arable fields seems plausible. Indeed, all four investigated taxonomic groups were dominated by only a few species, and these occurred frequently under high management intensity. Nevertheless, we expected agricultural management to act as a filter for the large number of uncommon or rare species, independent of geographic location and surrounding landscape. This was shown in plant abundance, plant species composition and all measurements of spider communities. Furthermore, individual agricultural management variables had significant impacts on plant species richness, bee abundance and bee species richness. In contrast, earthworm communities were largely unaffected by the agricultural management variables that were available in this study. However, in agreement with other studies across several regions (e.g. Concepción et al, 2012b; Báldi et al., 2013), the majority of variation in species communities was explained by region (in the geographic location variables group). This demonstrated that farmland species communities were samples of the regional species pool driven by agricultural management and surrounding landscape variables (Tscharntke et al., 2005).

5. Conclusions

This is a rare study that investigated contrasting taxonomic groups in arable fields across several European regions. The consideration of abundance, species richness and species composition clearly contributed to an information gain regarding community structures and allowed us to separate general from taxon-specific effects. As expected, plant, earthworm, spider and bee communities differed in their responses to geographic location, agricultural

management and surrounding landscape. One of the strongest general results of this study was the clear detrimental effect of mineral N input and pesticide applications on plant or bee abundance, respectively, as well as on species richness of plants and bees. Besides the significant agricultural management effects, this study revealed the predominant effect of geographic location, pointing out that regional conditions should be taken into account when designing measures to promote farmland species.

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Supplementary Material

Table S1: Numbers of investigated arable fields, species richness and abundance in the four study regions. Gamma species richness: The number of species found in all arable fields of the respective study region, in brackets the number of species found exclusively in the respective study region. Alpha species richness: The mean number of species per field ± standard error. Abundance: The mean cover of non-crop plants per field ± standard error and the mean number of animal individuals per field ± standard error, respectively.

Region		**Marchfeld**	**Southern Bavaria**	**Gascony**	**Homokhátság**
Number of fields		56	49	39	23
Plants	Gamma species richness	88 (35)	107 (40)	138 (68)	105 (52)
	Alpha species richness	5.54 ± 0.55	13.61 ± 1.18	12.82 ± 1.15	13.96 ± 1.01
	Abundance	30.02 ± 5.38	32.67 ± 5.17	79.15 ± 10.45	58.09 ± 8.39
Earth-worms	Gamma species richness	7 (2)	9 (2)	13 (8)	3 (1)
	Alpha species richness	1.84 ± 0.12	3 ± 0.18	4.64 ± 0.24	0.74 ± 0.18
	Abundance	7.91 ± 0.86	12.71 ± 1.4	36.54 ± 4.53	3.22 ± 1.12
Spiders	Gamma species richness	52 (16)	48 (21)	97 (64)	31 (14)
	Alpha species richness	3.8 ± 0.39	7.31 ± 0.54	6.97 ± 0.72	2.44 ± 0.56
	Abundance	8.16 ± 1.4	17.45 ± 1.84	13.28 ± 1.51	5.96 ± 2.09
Bees	Gamma species richness	16 (7)	14 (6)	48 (35)	16 (8)
	Alpha species richness	0.43 ± 0.13	0.49 ± 0.12	3.23 ± 0.57	0.87 ± 0.23
	Abundance	0.54 ± 0.18	0.67 ± 0.18	6.56 ± 1.32	1.04 ± 0.33

Table S2:Plant species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Plant species	**Marchfeld**	**Southern Bavaria**	**Gascony**	**Homokhátság**
Capsella bursa-pastoris	2	9	1	15
Chenopodium album	21	23	16	1
Cirsium arvense	26	1	14	1
Convolvulus arvensis	7	3	18	12
Dactylis glomerata	2	9	5	4
Fallopia convolvulus	1	24	9	3
Galium aparine	12	19	11	2
Lolium perenne	1	14	5	2
Medicago sativa	6	15	5	11
Papaver rhoeas	5	3	4	15
Plantago lanceolata	1	3	7	4
Polygonum aviculare	1	16	1	1
Sinapis arvensis	2	1	3	1
Alopecurus pratensis	1	1		1
Anagallis arvensis		4	15	1
Avena fatua	5	3	23	
Bromus sterilis	4		4	3
Conyza canadensis	2		2	2
Epilobium tetragonum	1	1	3	
Festuca pratensis	1	4	1	
Lactuca serriola	4		8	2
Lolium multiflorum	1	13	9	

Myosotis arvensis		18	5	1
Phleum pratense	1	7	3	
Plantago major		8	1	1
Ranunculus repens		4	3	1
Sonchus asper	1	8	11	
Stellaria media	19	2		8
Taraxacum officinale	5	1		6
Trifolium pratense	3	14	8	
Veronica arvensis		3	3	13
Veronica hederifolia	7	1		3
Veronica persica	4	16	2	
Vicia cracca		3	1	1
Vicia sativa	2	2	1	
Viola arvensis	8	1	1	
Acer campestre		1	1	
Achillea millefolium agg.		1	1	
Alopecurus myosuroides		3	1	
Ambrosia artemisiifolia	1			7
Anthemis arvensis		6		1
Anthemis ruthenica		1		3
Apera spica-venti		17		3
Arctium lappa	1		1	
Arenaria serpyllifolia	1			8
Artemisia vulgaris	1			2
Asperugo procumbens	1			1
Bromus hordeaceus			4	2
Bromus tectorum	3			7
Bryonia dioica	1		1	
Buglossoides arvensis	2			5
Calystegia sepium	3		4	
Carduus nutans			1	3
Centaurea cyanus	2	4		
Cichorium intybus			2	2
Consolida regalis	3			8
Cynodon dactylon			4	2
Daucus carota			2	1
Descurainia sophia	5			8
Echinochloa crus-galli		9	2	
Elymus repens		16		15
Equisetum arvense		25	1	
Eryngium campestre			2	2
Euphorbia helioscopia		3	6	
Geranium dissectum		6	6	
Holcus lanatus		1	3	
Lamium amplexicaule	7			9
Lamium purpureum		5		1
Lapsana communis		8	2	
Lathyrus pratensis	1		4	
Malva neglecta	2		1	
Medicago lupulina		3	7	
Melilotus officinalis		1		1
Mercurialis annua	5		5	
Poa annua		14	1	
Poa pratensis	1	8		

Poa trivialis		5	2	
Polygonum lapathifolium		15	2	
Polygonum persicaria		7	5	
Reseda lutea	1			2
Rumex acetosa		2	2	
Rumex crispus		14	11	
Senecio vernalis	1			6
Senecio vulgaris	1		2	
Setaria pumila			2	1
Sherardia arvensis		9	4	
Silene latifolia		1		9
Solanum nigrum	2	4		
Thlaspi arvense	1	5		
Trifolium campestre		1	3	
Trifolium repens		22	1	
Urtica dioica	1	1		
Valerianella locusta			1	2
Veronica polita			3	1
Vicia hirsuta		6	3	
Vicia sepium		1	1	
Vicia tetrasperma		7	2	
Acer pseudoplatanus		4		
Achillea collina				4
Agrostemma githago				1
Agrostis stolonifera			1	
Allium oleraceum			1	
Allium scorodoprasum				1
Althaea hirsuta			1	
Alyssum alyssoides				2
Amaranthus powellii	6			
Amaranthus retroflexus	5			
Anagallis foemina			7	
Anchusa arvensis	1			
Angelica sylvestris		1		
Anthemis austriaca	13			
Anthemis cotula			11	
Anthriscus caucalis			6	
Aphanes arvensis		8		
Arabidopsis thaliana				1
Arabis hirsuta				1
Arrhenatherum elatius			4	
Atriplex patula			1	
Atriplex prostrata			1	
Avena sterilis	2			
Ballota nigra				1
Bellis perennis		1		
Betula pendula		1		
Brassica nigra			1	
Briza minor			1	
Bromus inermis	1			
Camelina microcarpa				4
Camelina sativa	1			
Cardaria draba				4
Carduus acanthoides	2			

Carex flacca				1
Carex stenophylla				1
Carum carvi		2		
Centaurea scabiosa		1		
Cerastium fontanum		4		
Cerastium glomeratum			2	
Cerastium semidecandrum				6
Chaenorrhinum minus			1	
Chamomilla recutita		19		
Chamomilla suaveolens		4		
Chenopodium ficifolium	4			
Chenopodium hybridum	2			
Chenopodium polyspermum		5		
Chondrilla juncea				1
Chrysopogon gryllus				1
Cirsium canum				1
Cirsium oleraceum		1		
Clematis vitalba	1			
Clover grass	1			
Clover lucerne	1			
Cornus sanguinea		1		
Crepis foetida			1	
Crepis vesicaria			1	
Datura stramonium	2			
Deschampsia cespitosa				1
Digitaria sanguinalis				1
Echium vulgare				1
Elytrigia repens			1	
Equisetum ramosissimum				1
Erodium cicutarium				1
Erophila verna				1
Erysimum diffusum				1
Euphorbia esula				1
Euphorbia exigua			3	
Euphorbia segetalis			1	
Euphorbia virgata				1
Fagopyrum esculentum	6			
Falcaria vulgaris				1
Festuca pseudovina				7
Fraxinus angustifolia			1	
Fraxinus excelsior	2			
Fumaria officinalis			1	
Fumaria vaillantii	1			
Galeopsis angustifolia			4	
Galeopsis speciosa			1	
Galeopsis tetrahit		8		
Galinsoga ciliata		5		
Galinsoga parviflora		1		
Galium spurium	1			
Galium verum				2
Geranium pusillum	1			
Geranium pyrenaicum		1		
Geranium rotundifolium			1	
Glyceria fluitans		1		

Gnaphalium uliginosum		1		
Heracleum sphondylium		1		
Holosteum umbellatum				2
Hordeum murinum				1
Hyoscyamus niger	1			
Juncus bufonius		2		
Kickxia elatine			3	
Kickxia spuria			7	
Koeleria cristata				1
Lactuca saligna			1	
Lamium galeobdolon		1		
Lappula heteracantha				1
Lathyrus hirsutus			1	
Lathyrus nissolia			2	
Lathyrus sativus	1			
Lathyrus tuberosus	2			
Legousia speculum-veneris		1		
Lens culinaris			1	
Leontodon saxatilis			1	
Lepidium perfoliatum				1
Lepidium ruderale				1
Linaria vulgaris			1	
Linum angustifolium			1	
Lotus corniculatus			4	
Malva sp			1	
Matricaria chamomilla	3			
Matricaria inodora				2
Matricaria maritima		14		
Matricaria recutita			1	
Medicago falcata				1
Medicago minima				1
Medicago polymorpha			2	
Medicago sp			1	
Melilotus alba		1		
Melilotus albus				1
Mentha arvensis		1		
Mentha longifolia		1		
Misopates orontium			1	
Myosotis stricta				1
Odontites rubra			1	
Ononis spinosa s. maritima v.				1
Persicaria maculosa	1			
Phalaris paradoxa			1	
Phleum sp		3		
Phragmites australis				2
Picris echioides			18	
Plantago maritima				1
Poa angustifolia				8
Poa bulbosa				1
Polygala amarella				1
Polygonum amphibium		1		
Potentilla anserina		1		
Potentilla reptans			8	
Prunella vulgaris			1	

Prunus spinosa			2	
Pulicaria dysenterica			1	
Quercus humilis			2	
Quercus robur			1	
Ranunculus acris		1		
Ranunculus arvensis			3	
Ranunculus sardous			1	
Ranunculus sp			1	
Raphanus raphanistrum		3		
Rapistrum rugosum s. rugosum			5	
Rhinanthus minor				1
Rorippa palustris		1		
Rubus caesius			11	
Rumex acetosella			3	
Rumex obtusifolius		28		
Salix caprea x aurita		1		
Salix purpurea		1		
Salsola kali				1
Salvia nemorosa	1			
Scleranthus annuus		1		
Scorzonera cana				2
Senecio jacobaea			3	
Serratula tinctoria				1
Silene alba	2			
Silene vulgaris	1			
Sisymbrium loeselii	1			
Sisymbrium orientale				4
Solidago gigantea	1			
Sonchus arvensis			2	
Stachys annua			2	
Stellaria graminea			1	
Stellaria pallida	1			
Symphytum officinale		1		
Tamus communis			1	
Taraxacum sp			1	
Trifolium arvense			1	
Trifolium dubium		2		
Trifolium hybridum			1	
Trifolium incarnatum			1	
Tripleurospermum inodorum	12			
Trisetum flavescens	1			
Valerianellla dentata		1		
Verbena officinalis			8	
Veronica agrestis	2			
Veronica triloba	5			
Veronica triphyllos				1
Vicia bithynica			5	
Vicia faba			2	
Vicia villosa				5
Viola kitaibeliana				3
Viola tricolor	1			
Vulpia bromoides			2	
Vulpia myuros			1	
Xanthium strumarium			2	

Table S3:Earthworm species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Earthworm species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Allolobophora caliginosa	41	44	35	7
Allolobophora rosea	41	29	18	8
Allolobophora chlorotica	8	9	33	
Octolasium lacteum	2	8	4	
Lumbricus castaneus		15	1	
Lumbricus terrestris	8	23		
Octolasium cyaneum		5	4	
Allolobophora cupulifera			1	
Allolobophora georgii				2
Allolobophora muldali			9	
Dendrobaena byblica	2			
Dendrobaena mammalis			4	
Lumbricus festivus	1			
Lumbricus friendi			22	
Lumbricus herculeus			1	
Lumbricus rubellus		13		
Octodrilus transpadanum		1		
Prosellodrilus fragilis			3	
Scheroteca savignyi			19	

Table S4: Spider species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Spider species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Erigone dentipalpis	9	3	7	3
Mangora acalypha	2	6	5	3
Meioneta rurestris	22	35	19	9
Neottiura bimaculata	6	28	8	6
Pachygnatha degeeri	14	34	6	2
Pardosa agrestis	14	4	2	1
Araeoncus humilis	17	17		2
Aulonia albimana	1		2	1
Bathyphantes gracilis	4	5	4	
Diplostyla concolor	1	6	7	
Euophrys frontalis	1		3	1
Mermessus trilobatus	5	15	1	
Microlinyphia pusilla	2	5		2
Oedothorax apicatus	32	36	21	
Pachygnatha clercki	1	2	1	
Pardosa prativaga	3	1	3	
Pelecopsis parallela		1	6	1
Phylloneta impressa	1	13		1
Porrhomma microphthalmum	5	3	3	
Tenuiphantes tenuis	11	19	26	
Xysticus kochi	4	1	3	

Argiope bruennichi		2	2	
Cryptachaea riparia	2	2		
Dicymbium nigrum brevisetosum		3	1	
Drassyllus pusillus	1		1	
Enoplognatha thoracica	3		1	
Erigone atra	7	31		
Ero furcata	1		1	
Gnathonarium dentatum	1	1		
Haplodrassus minor	2			2
Hypsosinga pygmaea	1		1	
Maso sundevalli	2		2	
Meioneta simplicitarsis	1			2
Micrargus herbigradus		1	1	
Micrargus subaequalis	6		2	
Pardosa palustris	2	4		
Phrurolithus festivus			8	1
Pisaura mirabilis			3	1
Robertus arundineti	6		1	
Sibianor aurocinctus			3	1
Tenuiphantes flavipes	1		1	
Tibellus oblongus	1		1	
Trochosa ruricola	1	1		
Acartauchenius scurrilis				1
Aculepeira ceropegia		2		
Agraecina lineata			3	
Araneus diadematus				1
Araniella cucurbitina		1		
Argenna subnigra	2			
Bathyphantes similis				3
Brommella falcigera	1			
Centromerita bicolor		1		
Centromerus sp2			1	
Chalcoscirtus infimus			1	
Cheiracanthium pennyi				1
Clubiona pseudoneglecta			7	
Clubiona reclusa		1		
Clubiona subtilis				1
Cresmatoneta mutinensis			2	
Crustulina guttata			1	
Crustulina sticta			1	
Cyclosa oculata			1	
Dictyna arundinacea				1
Dictyna sp			1	
Diplocephalus cristatus		1		
Diplocephalus graecus			2	
Dismodicus bifrons		1		
Drassyllus lutetianus			1	
Drassyllus praeficus			1	
Drassyllus villicus			1	
Enoplognatha latimana			1	
Enoplognatha mordax			1	
Enoplognatha ovata			1	
Entelecara flavipes		1		
Episinus truncatus			3	

Erigonella hiemalis		2		
Ero aphana			1	
Euophrys gambosa			1	
Gibbaranea bituberculata			1	
Gongylidiellum latebricola		1		
Gongylidiellum murcidum	1			
Hahnia candida			1	
Hahnia nava	1			
Hahnia pusilla		1		
Harpactea hombergi			1	
Heliophanus cupreus			1	
Heliophanus flavipes			1	
Hypsosinga sanguinea	2			
Leptorhoptrum robustum		1		
Linyphia triangularis		1		
Linyphiidae			1	
Liophrurillus flavitarsis			1	
Marpissa nivoyi			1	
Maso gallicus			1	
Meioneta mollis			7	
Meioneta saxatilis	1			
Metopobactrus prominulus			1	
Micrargus apertus			1	
Microlinyphia impigra	1			
Microneta viaria				1
Minyriolus pusillus		1		
Neoscona adianta				1
Neoscona byzanthina			1	
Neriene clathrata			1	
Neriene furtiva			1	
Oedothorax fuscus		7		
Ostearius melanopygius			3	
Ozyptila atomaria			1	
Ozyptila brevipes			1	
Ozyptila simplex			4	
Palliduphantes alutacius			1	
Panamomops sulcifrons			3	
Pardosa hortensis			4	
Pardosa lugubris	1			
Pardosa proxima			11	
Pardosa saltans			1	
Pardosa vittata			5	
Pelecopsis bucephala			1	
Philodromus pulchellus			2	
Phrurolithus minimus			1	
Phrurolithus nigrinus			5	
Pirata latitans		1		
Porrhomma oblitum		3		
Robertus neglectus		4		
Runcinia grammica				2
Silometopus reussi	3			
Singa hamata				1
Sitticus rupicola				1
Steatoda phalerata			1	

Talavera aequipes	1				
Tenuiphantes zimmermanni			1		
Tetragnatha pinicola		5			
Thanatus atratus			2		
Theridion impressum			2		
Theridion nigrovariegatum			1		
Theridion uhligi Martin 1974			1		
Thomisus onustus				1	
Tibellus maritimus				1	
Tiso vagans		3			
Titanoeca tristis			1		
Tmarus stellio			1		
Trachelas minor			2		
Trichoncoides piscator	1				
Trichoncus hackmani				1	
Trichoncus saxicola			1		
Walckenaeria capito			1		
Walckenaeria dysderoides	1				
Walckenaeria nudipalpis		1			
Walckenaeria vigilax		4			
Xerolycosa miniata	1				
Xysticus striatipes	1				
Xysticus ulmi	1				
Zelotes civicus			3		
Zelotes gracilis	1				
Zelotes tenuis			1		
Zora parallela			1		
Zora pardalis			1		
Zora spinimana			1		

Table S5: Bee species list. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and secondly to the alphabet.

Bee species	Marchfeld	Southern Bavaria	Gascony	Homokhátság
Bombus terrestris	3	3	14	1
Andrena labialis	1	1	1	
Bombus lapidarius	3	2	8	
Bombus pascuorum	1	2	6	
Bombus sylvarum		1	2	3
Andrena decipiens			1	1
Andrena dorsata	1			1
Andrena flavipes		2	3	
Andrena ovatula			1	3
Bombus hortorum		1	1	
Bombus ruderatus	1		2	
Eucera nigrescens	3			1
Halictus simplex	2		11	
Lasioglossum pauxillum		2	4	
Megachile leachella			1	1
Rophites canus	2			1
Andrena agilissima			1	
Andrena barbilabris				1
Andrena impunctata			1	
Andrena producta	1			
Andrena sp				1
Andrena variabilis			2	
Andrena wilkella			2	
Anthidium oblongatum			1	
Bombus bohemicus		1		
Bombus confusus			2	
Bombus hypnorum		2		
Bombus vestalis	1			
Coelioxys afra			1	
Colletes similis			1	
Dasypoda altercator			1	
Eucera chrysopyga	1			
Eucera clypeata			3	
Eucera longicornis	1			
Eucera taurica			1	
Halictus eurygnathus				1
Halictus maculatus			2	
Halictus rubicundus	1			
Halictus scabiosae			5	
Halictus seladonius			1	
Halictus sexcinctus				1
Halictus smaragdulus			2	
Halictus tetrazonius gr				1
Halictus tumulorum			3	
Halictus vestitus			1	
Heriades truncorum			1	
Hylaeus gredleri	1			
Lasioglossum calceatum		3		
Lasioglossum corvinum			1	

Lasioglossum discum				1	
Lasioglossum fulvicorne		1			
Lasioglossum glabriusculum			5		
Lasioglossum griseolum				1	
Lasioglossum interruptum			1		
Lasioglossum lativentre			1		
Lasioglossum leucozonium			2		
Lasioglossum malachurum			9		
Lasioglossum morio			2		
Lasioglossum politum			3		
Lasioglossum punctatissimum			1		
Lasioglossum puncticolle			4		
Lasioglossum sp			2		
Lasioglossum villosulum			4		
Lasioglossum zonulum		2			
Megachile centuncularis			1		
Megachile opacifrons			1		
Megachile rotundata			1		
Melitta leporina		1			
Melitturga clavicornis				1	
Rophites algirus	1				
Sphecodes ephippius			1		
Xylocopa violacea			1		

CHAPTER 2

Which Factors Structure Bee, Spider, Earthworm and Plant Communities in European Grasslands?

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Abstract

Wild bees, spiders, earthworms and plants contribute considerably to biodiversity in grasslands and fulfil vital ecological functions. They also provide valuable services to agriculture, such as pollination, pest control and maintenance of soil quality. We investigated the responses of wild bees, spiders, earthworms and plants to geographic location, agricultural management and surrounding landscape variables across a dataset of 357 grassland fields

within 88 farms in six European regions. Regions and taxonomic groups were selected to have contrasting properties, in order to capture the multiple facets of European grasslands. Indeed, geographic location had a dominant effect on the fauna and flora communities. Depending on the taxonomic group, various agricultural management and surrounding landscape variables had an additional significant effect on species richness and/or abundance. Bee species richness and abundance decreased with increasing number of mechanical field operations (e.g. cutting). Spider species richness and abundance were unrelated to measured aspects of agricultural management or to surrounding landscape variables. Earthworm abundance increased with increasing nitrogen input but earthworm species richness did not. Plant species richness decreased with increasing nitrogen input and increased when there were woody habitats in the surroundings. Investigating multiple regions, taxonomic groups and aspects of fauna and flora communities allowed identifying the main factors structuring communities, which is necessary for designing appropriate conservation measures and ensuring continued supply of services.

Zusammenfassung

Wildbienen, Spinnen, Regenwürmer und Pflanzen machen einen bedeutenden Teil der Biodiversität in landwirtschaftlich genutztem Grünland aus und bilden eine wichtige Grundlage für ökologische Dienstleistungen. Dazu gehören z.B. Bestäubung, biologische Schädlingsbekämpfung und der Erhalt der Bodengesundheit. Wir untersuchten, inwiefern die vier taxonomischen Gruppen von der geografischen Lage, von Bewirtschaftungs- und von Umgebungsfaktoren abhängig sind. In die Studie gingen Daten aus sechs europäischen Regionen ein, die in 88 landwirtschaftlichen Betrieben auf insgesamt 357 Mähwiesen und Weiden erhoben wurden. Die Regionen und taxonomischen Gruppen wurden gezielt

ausgewählt, um eine möglichst breite Vielfalt im europäischen Agrargrünland abzudecken. Tatsächlich beeinflusste die geografische Lage die Artengesellschaften am stärksten. Je nach taxonomischer Gruppe hatten verschiedene Bewirtschaftungs- und Umweltfaktoren zusätzlich einen signifikanten Effekt auf Artenvielfalt und/oder Abundanz. Bei den Bienen nahmen Artenvielfalt und –abundanz mit der Anzahl maschineller Bearbeitungen (z.B. Schnitt) pro Jahr ab. Weder die Spinnenartenvielfalt noch die –abundanz waren abhängig von den erhobenen Bewirtschaftungs- oder Umweltfaktoren. Bei den Regenwürmern erhöhte sich die Abundanz mit dem Stickstoffeintrag, nicht aber die Artenvielfalt. Die Artenvielfalt der Pflanzen nahm mit dem Stickstoffeintrag ab und mit dem Gehölzanteil in der Umgebung zu. Die Untersuchung von mehreren Regionen, taxonomischen Gruppen und Aspekten von Artengesellschaften erlaubte die wichtigsten Einflussfaktoren auf Artengesellschaften zu erkennen. Diese Resultate können dazu beitragen wirksame Massnahmen für den Erhalt der Biodiversität und die Sicherstellung der ökologischen Dienstleistungen zu erarbeiten.

Keywords

Species composition, Species richness, Abundance, Partitioning of variation

1. Introduction

Permanent grasslands cover around one third of European agricultural land and provide habitat for fauna and flora communities that fulfil vital ecological functions such as primary production, decomposition, predation or pollination (Hooper et al. 2005). There is general consensus that species-rich permanent grasslands should be maintained or regenerated to conserve biodiversity and associated ecological goods and services (e.g. Singh et al. 2014). Whereas patterns and determinants of plant diversity in grasslands have been reviewed and generalized (e.g. Gaujour et al. 2012), most faunal community studies have concentrated on one or few taxonomic groups in a restricted geographic extent (e.g. Power et al. 2012).

However, determining general and specific factors that structure communities and related ecological functions requires investigations of various taxonomic groups at large spatial extent (Tscharntke et al. 2012). For instance, communities may react contrastingly between regions because biogeographic conditions, historical progression of land use and agricultural management determine the species pool and available habitats (Báldi et al. 2013; Batáry et al. 2010; Concepción et al. 2012; Jeanneret et al. 2003; Paoletti et al. 1995).

In order to analyse how geographic location, agricultural management and surrounding landscape affect species diversity in permanent grasslands, we sampled four contrasting taxa in 357 fields in six regions across Europe. We selected wild bees, spiders, earthworms and plants because they differ with regard to trophic level, ecological function and habitat requirements. Bees as pollinators are affected by agricultural management shortening the supply of food and nesting sites (e.g. Kremen et al. 2007). The response of spiders as predators to agricultural management and surrounding landscape characteristics depends on their hunting strategy and mobility (e.g. Samu et al. 1999). Earthworms as decomposers are strongly influenced by soil conditions, although individual species react differently to agricultural management (Paoletti 1999), whilst plants as primary producers decrease in species richness with management intensity and landscape homogeneity (Gaujour et al. 2012; Socher et al. 2012).

Environmental conditions might differently affect aspects of communities and taxonomic groups (Báldi et al. 2013; Dornelas et al. 2014; Grenouillet et al. 2002; Jeanneret et al. 2003). Therefore, analysing community structures in terms of several aspects, e.g. species composition, species richness and abundance of individuals per taxonomic group, provides a substantial information gain compared to the consideration of only one aspect. Accordingly, we partitioned the variation in species composition, species richness and abundance of the

four taxonomic groups into geographic location, agricultural management and surrounding landscape. Because European grasslands are diverse in land use history and environmental conditions (Batáry et al. 2010), we expected a predominant response of species composition to geographic location. Further, because habitat destruction and intensified agricultural management were found to reduce species diversity worldwide (Millenium Ecosystem Assessment 2005), we hypothesized that agricultural management and surrounding landscape would generally affect species richness and abundance, independent of geographic location. However, since grasslands in North, South and Western Europe are generally more intensively managed than grasslands in Central and Eastern Europe (Batáry et al. 2010), interactions between geographic location and agricultural management are likely to exist. In addition, we assumed that bees, spiders, earthworms and plants would respond differently to individual agricultural management and surrounding landscape variables because of contrasting ecological requirements.

2. Materials and Methods

Data collection was part of the EU-FP7 project BioBio, which developed biodiversity indicators for farmland monitoring (Herzog et al. 2012). This study investigated 357 grassland fields in six European regions: Stalden (Switzerland), Southern Bavaria (Germany), Gascony (France), Homokhátság (Hungary), Northern Hedmark (Norway) and Wales (United Kingdom, see Table 1). In each region, up to 19 study farms (half of them organically managed) were randomly selected and all permanent grasslands classified into habitat types according to (1) the dominant Raunkiær plant life form, (2) soil humidity, acidity and nutrient supply and (3) the occurrence of trees (Bunce et al. 2008; Dennis et al. 2012). For each available habitat type per farm, one field was randomly selected for species sampling.

Table 1: Geographic coordinates and environmental and agricultural characteristics of the study regions. UAA = utilized agricultural area.

Region	**Stalden**	**Southern Bavaria**	**Gascony**	**Homok-hátság**	**Northern Hedmark**	**Wales**
Country	CH	D	F	H	N	UK
Latitude	N 46° 54’	N 48° 24’	N 43° 24’	N 46° 42’	N 62° 24’	N 52° 30’
Longitude	E 8° 12’	E 11° 18’	E 0° 48’	E 19° 36’	E 11° 6’	W 3° 48’
Altitude [m]	605 - 1133	350 - 500	197 - 373	93 - 168	488 - 886	450 - 1085
Climate	Alpine	Continental	Sub-Mediterranean	Pannonian	Boreal	Atlantic
Annual precipitation [mm]	1300	800	680	550	470	1500
Mean annual temp. [°C]	5.6	8.5	13	10.4	0.4	10
Soil	Fluvisol, Podzoluvisol	Cambisol, Luvisol	Orthic Rendzina, Cambisol	Arenosol, Cambisol	Podzol, Regosol	Cambisol, Gelysol, Podzol
Grassland [% of UAA of investigated farms]	100	31	8	76	88	86
# Investigated grassland fields	65	32	61	88	62	49

The four taxonomic groups were sampled from spring to early autumn 2010 according to standardized protocols (Dennis et al. 2012). Bees were sampled on three dates during good weather conditions with a handheld net along a 100 m × 2 m transect for 15 minutes. The bumblebee species *Bombus lucorum* and *B. terrestris* were combined in one (*B. terrestris gr.*), since they are very difficult to distinguish from one another. Honeybees (*Apis mellifera*) were excluded from the analysis because occurrence of domestic hives can override all other influences. Spiders were sucked on three dates from soil surface and vegetation within five circular areas of 35.7 cm diameter each, using a modified leaf blower. Earthworms were collected at three random locations of 30 cm × 30 cm per field by first pouring a solution of allyl isothiocyanate (0.1 g/l) into a metal frame to collect those coming to the surface, and afterwards by sorting a 20 cm deep soil core by hand. Juvenile worms (without clitellum) were excluded from the analysis. Plant species and their respective ground cover were recorded in one plot of 10 m × 10 m per field (total cover could exceed 100% if plants overlapped). Species of all four taxonomic groups were identified to the species level by specialists.

Species composition (species list and abundance), species richness (total number of species observed) and abundance (total number of individuals for faunal groups and the total percentage cover for plants) for each taxonomic group were investigated as response variables per field (i.e. all faunal subsamples were combined at field scale). Because sampling effort in terms of area, time and sampling period was equal across all fields, the chance to detect individuals was it also (Gotelli et al. 2001). Hence, we analysed the observed species richness.

Eight potential structuring variables were assembled into the three groups: geographic location variables, agricultural management variables and surrounding landscape variables (Table 2). Geographic location was described by the study region and the farm to which the investigated field belonged to. Agricultural management was described by total nitrogen (N) input, number of mechanical field operations and grass use intensity in 2010, recorded in structured interviews with farmers. Grass use intensity was estimated by combining the number of cuts and the stocking rate (cattle and sheep) relative to the duration of the vegetation period in the different regions (i.e. very low, low, moderate or high, see Appendix B in Supplementary Material). Surrounding landscape was described with the Shannon diversity index of habitats, the percentage of woody habitats and the percentage of grassland habitats in a buffer zone of 250 m around each investigated field (see Lüscher et al. 2014 for details). The buffer zone size was a compromise between radii of action of the four contrasting taxonomic groups (Gaba et al. 2010; Schmidt et al. 2008; Zurbuchen et al. 2010).

Table 2: Agricultural management and landscape characteristics used as explanatory variables. For grass use intensity the number of investigated fields in the four grass use intensity classes is indicated. Grass use intensity classification was context dependent (see text for explanation and Appendix A in Supplementary Material). For the other variables the mean (standard error) of the investigated fields is shown.

Region (# Farms)		**Stalden (19)**	**Southern Bavaria (15)**	**Gascony (12)**	**Homok-hátság (18)**	**Northern Hedmark (12)**	**Wales (12)**
Agricultural management	Grass use intensity [# fields]						
	- "Very low"	6	5	53	24	20	8
	- "Low"	22	17	8	16	35	5
	- "Moderate"	21	6	0	4	6	5
	- "High"	16	4	0	44	1	31
	Total nitrogen input [kg/ha]	72 (10)	90 (17)	1 (1)	0	39 (8)	5 (4)
	Mineral N [% of kg total N in region]	1	52	100	NA	45	30
	# Mechanical field operations	8 (1)	17 (2)	3 (0)	0	2 (0)	0
Surrounding landscape	H[1] of surrounding habitats	1.06 (0.02)	1.05 (0.04)	0.73 (0.04)	0.75 (0.04)	0.71 (0.04)	0.33 (0.04)
	Area of woody habitat [%]	23 (2)	16 (3)	13 (1)	9 (1)	53 (3)	11 (2)
	Area of grassland [%]	63 (2)	29 (3)	14 (2)	59 (3)	43 (3)	86 (2)

[1] H = Shannon diversity index

Partitioning of variation (Legendre and Legendre 2012) was used to separate the effects of geographic location, agricultural management and surrounding landscape on species composition, species richness and abundance. The percentages of explained variation were calculated as adjusted R^2 and significance was tested by partial redundancy analysis with 999 permutations (RDA). In order to comply with statistical assumptions, species composition data were Hellinger-transformed (Legendre and Gallagher 2001). Species richness and abundance were log-transformed after adding a constant c = 0.5 (½ of the smallest non-zero integer value).

Effects of individual explanatory variables on species richness and abundance were analysed using generalized linear mixed-effects models (see Appendix B for detailed formula). A

negative binomial distribution was used to account for overdispersion. Agricultural management and surrounding landscape variables were treated as fixed effects and two-way interactions were included if significant. Region was always included as random intercept. Farm was also included if it improved the model fit significantly. Random slopes for the numerical explanatory variables were always tested. The level "very low" was used as the baseline to test effects of grass use intensity. Models were reduced based on Akaike's information criterion corrected for small samples (Burnham and Anderson 2002). The significance of effects was assessed using likelihood-ratio tests.

All analyses were performed in R 2.15.3 using packages vegan 2.0-6, vennerable, plotrix, glmmADMB 0.7.3, AICcmodavg 1.27 and lmtest (R Development Core Team 2012).

3. Results

Across all 357 fields, a total of 2853 bees, 9152 adult spiders and 8358 adult earthworms were sampled. We identified 208 bee, 356 spider, 28 earthworm and 797 plant species (see Appendix F for complete species lists). Two bumblebee, *Bombus pascuorum* and *B. terrestris gr.*, (Fig. 1a), two spider, *Erigone dentipalpis* and *Pardosa palustris* (Fig. 1b) and two earthworm species, *Allolobophora caliginosa* and *A. rosea* (Fig. 1c), occurred in all regions accounting for 24%, 4% and 51% of all individuals per region on average, respectively. Amongst plants, 14 species occurred in all six regions (Fig. 1d), accounting for 24% of the total plant cover per region on average. The most abundant of them were *Trifolium repens, Dactylis glomerata* and *Poa pratensis*.

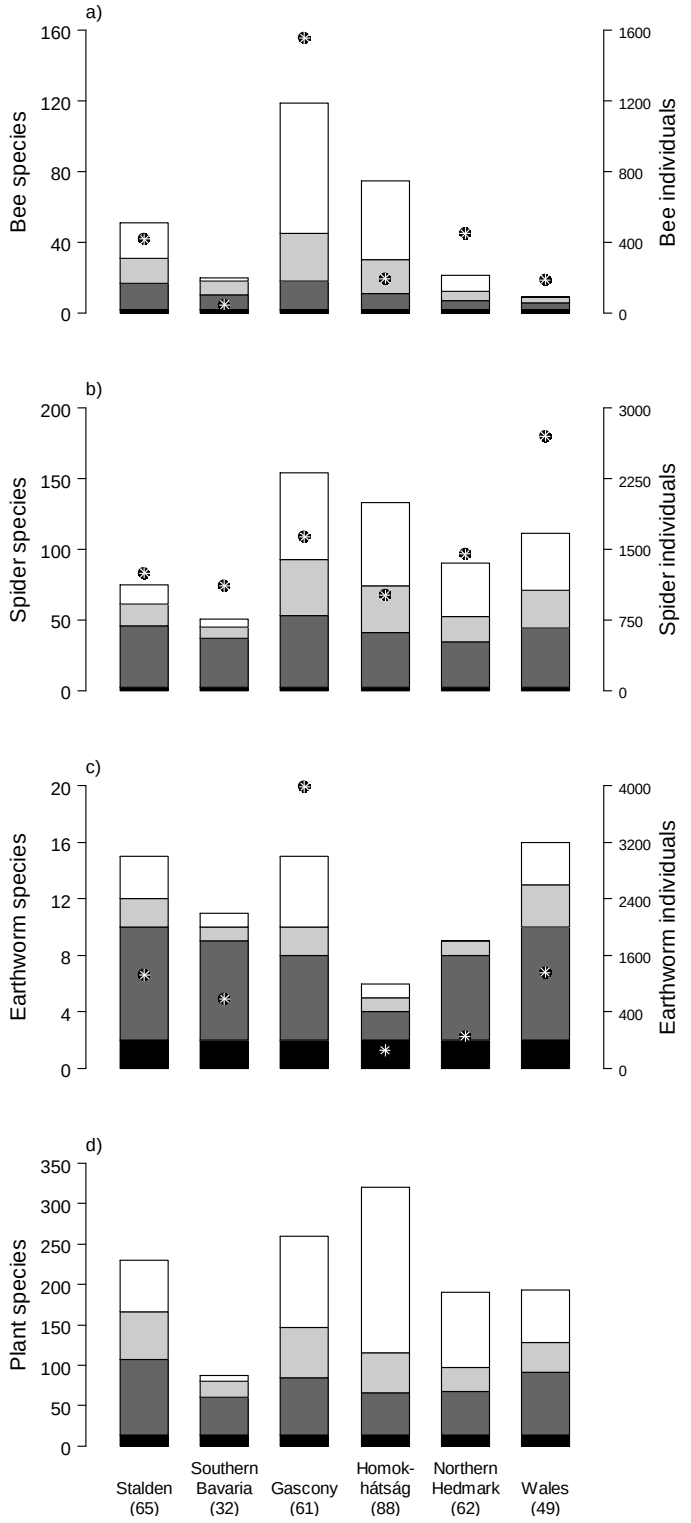

Fig. 1: Total number of (a) bee, (b) spider, (c) earthworm and (d) plant species in the study regions. Shading indicates the number of species occurring: in all six regions (black), in three, four or five regions (dark grey), in two regions (light grey), exclusively in the corresponding region (white). White stars indicate the total number of (a) bee, (b) spider and (c) earthworm individuals in each region. The number of investigated fields per region is indicated in brackets.

The total number of species and individuals of the taxonomic groups varied across regions (Fig. 1, this was also the case for the species richness rarefied to the minimal number of sampled fields per region, i.e. 32 fields) and was generally high in the Gascony region. Bee species richness was lower in regions at higher latitudes (Northern Hedmark and Wales) than in regions further south. Earthworm species richness was lower in regions with a low level of annual precipitation (Homokhátság and Northern Hedmark). In Southern Bavaria, the number of exclusive species was generally low. The large biogeographic gradient spanned by all six regions (Table 1) was also reflected by region-specific management practices (e.g. exclusively cut grasslands in Gascony and mainly grazed grasslands in Homokhátság, Northern Hedmark and Wales).

Partitioning of variation revealed that species composition of all four taxonomic groups was predominantly structured by geographic location (16.4% of variation explained on average, Fig. 2). In addition, small percentages of variation in species composition of bees, spiders and plants were significantly explained by agricultural management alone (0.9%, 0.6% and 1.4%, respectively) and surrounding landscape alone (0.6%, 0.2% and 0.4%, respectively). For earthworm composition, agricultural management alone and surrounding landscape alone did not explain any significant part of the variation.

Variations in species richness and abundance were predominantly explained by geographic location alone (38% and 37% on average, respectively). Agricultural management and surrounding landscape, each considered alone, explained significant percentages of variation in plant species richness only (2.4% and 1.7%, respectively).

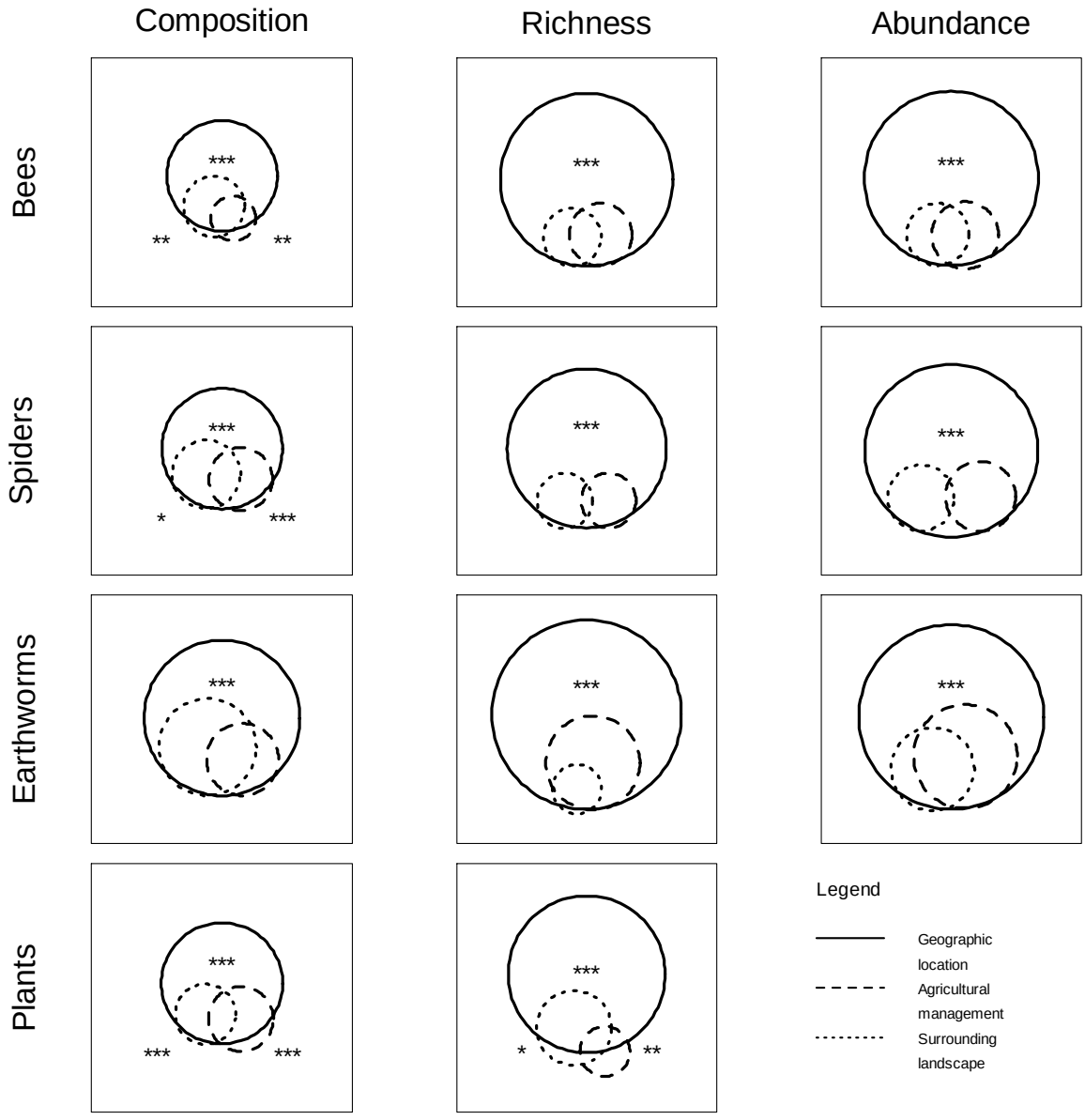

Fig. 2: Partitioning of variation into species composition, species richness and abundance of bees, spiders, earthworms and plants explained by geographic location (region and farm), agricultural management (total nitrogen input, number of mechanical field operations and grass use intensity) and surrounding landscape (Shannon diversity index of habitats, percentage of woody habitats and percentage of grassland habitats in a buffer zone of 250 m) derived from partial redundancy analysis. The area of the circles is proportional to the percentage of variation explained by the respective explanatory variable group. Overlapping indicates the variation explained by two or three variable groups together. Each box accounts for the total variation (100 %), i.e. the area outside of the circles represents the amount of unexplained variation. Stars indicate the significance of the percentage of variation explained by one explanatory group, independently of the others: * = $p < 0.05$, ** = $p < 0.01$, *** = $p \leq 0.001$.

There were strong regional differences in the effects of the tested explanatory variables on species richness and abundance of the four taxonomic groups (see results of regional models in Appendix C). Analysis of detailed explanatory variables showed that bee species richness and abundance decreased with the number of mechanical field operations (Table 3). Earthworm abundance increased with nitrogen input, and plant species richness decreased with nitrogen input. Further, plant species richness was positively affected by the presence of woody habitats in the surrounding landscape. Curves of relationships are shown in Appendix D. No significant effects of agricultural management and surrounding landscape variables were found for spider and earthworm species richness or for spider abundance.

Table 3: Effects of geographic location, agricultural management and surrounding landscape variables on (a) the species richness of bees, spiders, earthworms and plants, and (b) the abundance of bees, spiders and earthworms estimated using binomial generalized mixed-effects models. Standard deviation of random effects and estimates of fixed effects in the best fitting model are shown. P-values were calculated from likelihood-ratio tests and significances indicated as ns = not significant, . = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p \leq 0.001$.

		Random effects		Fixed effects				Neg. binomial parameter
		Region [SD]	Farm [SD]	N input [kg*ha^{-1}] (*linear func.*)	N input [kg*ha^{-1}] (*quadr. func.*)	# Mechanical field operations (*quadr. func.*)	Woody habitats in the surroun-dings [%]	
a)	Bees	0.637	0.310			-0.001496 **		7.5 (± 2.1)
	Spiders	0.321	0.220					10.0 (± 1.9)
	Earthworms	0.643						403.4 (± 0.4)
	Plants	0.236	0.121	-0.003579 ***	0.000009**		0.0041***	16.1 (± 2.3)
b)	Bees	0.848	0.386			-0.00177 **		1.840 (± 0.2.)
	Spiders	0.487	0.359					2.7 (± 0.3)
	Earthworms	0.909		0.006034**	-0.000018*			1.3 (± 0.1)
	Earthworms [1)]	0.908		0.00785 ns	- 0.0000463 .			1.3 (± 0.1)
	Earthworms [2)]	0.912		0.00704 *	- 0.0000208 ns			1.3 (± 0.1)

[1)] exclusively mineral N input ,[2)] exclusively organic N input

4. Discussion

In many European countries, permanent grasslands occupy sites with limited productivity or other constraints to arable production. Because management is rather stable over time, communities adapt to local environmental conditions. This explains the detected strong effect of geographic location, which is much stronger in grasslands than in arable fields (Báldi et al. 2013; Batáry et al. 2010; Concepción et al. 2012; Lüscher et al. 2014; Richner et al. submitted). Bee species richness decreased to the North and earthworm species richness with reduced annual precipitation as well as in the more Eastern regions probably due to unfavourable soil conditions. Proximity to the Mediterranean biodiversity hotspot might have fostered the high number of exclusive species in Gascony. In Homokhátság, grassland habitats covered a broad gradient from waterlogged to extremely dry and from acid to basic and saline soil conditions. Therefore, a high variety of exclusive species, mainly plants, occupied the different niches there.

In our broad-scale assessment, consistent effects of agricultural management and surrounding landscape on grassland communities across Europe are surprisingly rare. This suggests distinct impacts of similar agricultural practices, both in past and present, on communities across the investigated fields and regions. Further, the lack of overall effect of surrounding landscape indicate large-scale landscape patterns and characteristics such as connectivity to co-determine the regional and local species pool rather than the adjacent surroundings (see also Gaujour et al. 2012).

However, specific drivers for the diversity of particular taxonomic groups were identified. Bee species richness and abundance were negatively affected by the number of mechanical field operations, which suggests direct damage by machines and the decrease of blossom cover, and thus reduced food supply by an intensive cutting regime (Kremen et al. 2007). In

addition, plants may have fewer reserves to invest in pollen and nectar production with frequent cutting, reducing food availability for bees. Earthworm abundance increased with (organic) nitrogen input (and decreased with mineral one), probably due to the high organic matter supply in intensively fertilized grassland compared to steep pastures with shallow soils or extremely dry or wet sites, which were less fertilized (Paoletti 1999). Plant species richness was reduced by nitrogen input, in accordance with numerous other studies, e.g. Socher et al. (2012). Woody habitats in the surroundings increased plant species richness what might be linked to the general higher biodiversity levels in complex than in simple landscapes (Batáry et al. 2011). Over all regions, we did not find spider species richness and abundance correlated to agricultural management or surrounding landscape, in contrast to significant effects shown for crop field communities (e.g. Schmidt et al. 2005). Nevertheless, we found effects of the surroundings, e.g. the amount of woody and grassland habitats, in some regions. Because each taxonomic group was structured by specific factors, correlations between the taxonomic groups were rare (see Appendix E).

We conclude that, in order to develop measures for the promotion of biodiversity in grasslands across Europe, regional characteristics must be considered besides basic, general measures, like the reduction of mechanical field operations and mineral nitrogen input, appropriate input of organic nitrogen and careful consideration of landscape complexity. However, the concrete steps must be developed region specific. This gives high responsibility for states in regulating the use of agricultural subsidies, for example under the Common Agricultural policy of the EU. Our study highlights that broad-scale, multi-taxon investigations are vital to detect regional peculiarities, strengths and potentials in terms of grassland biodiversity. Such knowledge allows then implementation of region-specific measures to promote biodiversity conservation and associated ecological goods and services.

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Supplementary information

Appendix A

Table S1: Duration of vegetation period (number of days with mean temperature > 5° C) for each study region and its classification into difficulty categories regarding climate conditions that affect farmers' bases for production: 1 = best production bases (> 200 days), 2 = slightly restricted production bases (180 – 200 days), 3 = restricted production bases (160 – 180 days), 4 = difficult production bases (< 160 days).

Region	Duration of vegetation period [# days]	Difficulty category
Stalden	180	2
Southern Bavaria	240	1
Gascony	365	1
Homokhátság	200	2
Northern Hedmark	120	4
Wales	210	1

Formula

Formula to calculate the stocking rate (SR) on field i:

$$SR_i = \frac{1}{a_i * p_i} * LU_i * d_i$$

for a_i: the area of field i, for p_i: the duration of the vegetation period, for LU_i: the number of livestock units grazing on field i, and for d_i: the number of days LU_i was grazing on field i.

Table S2: Intensity classes for grazing.

Stocking rate SR	Intensity class
0 < x <= 1	Very low
1 < x <= 2	Low
2 < x <= 3	Moderate
3 < x	High

Table S3: Intensity classes for cutting.

Difficulty category	# Cuts	Intensity class
1	0 < x <= 1	Very low
1	1 < x <= 3	Low
1	3 < x <= 4	Moderate
1	4 < x	High
2	0 < x <= 1	Very low
2	1 < x <= 2	Low
2	2 < x <= 3	Moderate
2	3 < x	High
4	0 < x <= 1	Low
4	1 < x <= 2	Moderate
4	2 < x	High

Table S4: Combined intensity classes.

Intensity class cutting	Intensity class grazing	Combined intensity class
0	0	Very low
0	Very low	Very low
Very low	0	Very low
Very low	Very low	Low
0	Low	Low
Low	0	Low
Very low	Low	Low
Low	Very low	Low
Low	Low	Moderate
0	Moderate	Moderate
Moderate	0	Moderate
Very low	Moderate	Moderate
Moderate	Very low	Moderate
Low	Moderate	Moderate
Moderate	Low	Moderate
Moderate	Moderate	High
0	High	High
High	0	High
Very low	High	High
High	Very low	High
Low	High	High
High	Low	High
Moderate	High	High
High	Moderate	High

Appendix B

Model specification for generalized linear mixed-effects models

Best fitting model for bee, spider, earthworm and plant species richness and bee, spider and earthworm abundance, respectively.

Bee species richness	~ # Mechanical field operations (*quadr. func.*) + (1|Region) + (1|Farm)
Bee abundance	~ # Mechanical field operations (*quadr. func.*) + (1|Region) + (1|Farm)
Spider species richness	~ (1|Region)
Spider abundance	~ (1|Region) + (1|Farm)
Earthworm species richness	~ (1|Region)
Earthworm abundance	~ Nitrogen input (*linear func.*) + Nitrogen input (*quadr. func.*) + (1|Region)
Plant species richness	~ Nitrogen input (*linear func.*) + Nitrogen input (*quadr. func.*) + Woody habitats in the surroundings + (1|Region) + (1|Farm)

Appendix C

Table S5: Effects per region of geographic location, agricultural management and surrounding landscape variables on the species richness and abundance of a) bees, b) spiders, c) earthworms and d) plants (only richness) estimated using binomial generalized mixed-effects models. Estimates of fixed effects in the best fitting model are shown. P-values were calculated from likelihood-ratio tests. Signs (+ and –) indicate positive and negative effects. Significances are indicated as ns = not significant but included in best fitting model, * = $p < 0$, ** = $p < 0.01$ and *** = $p \leq 0.001$. Legend for abbreviations in the end.

		Random effects	Fixed effects																					Neg. binomial parameter
		Farm	N	N *qf*	Fo	Fo *qf*	"L"	"M"	"Hi"	H[1]	H[1] *qf*	W	W *qf*	G	G *qf*	I1	I2	I3	I4	I5	I6	I7	I8	I9	
a) Bees	Richness																							
	S					- **																		403.43 (± 1.031)
	SB		- *									- **	+ **											2.121 (± 1.739)
	G																							3.422 (± 0.911)
	H	0.521																						2.724 (± 1.373)
	NH																							6.012 (± 3.454)
	W														- *									24.876 (± 72.322)
	Abundance																							
	S					- ***																		18.574 (± 13.277)
	SB		- **		+ ns		+ **	+ *	+ *	- ns		- ns	+ **	+ ns		+ **	+ *	- ns	- *	+ ns	- *	- ns			403.430 (± 2.822)
	G																							1.275 (± 0.237)
	H	0.683																						2.046 (± 0.821)
	NH																							1.295 (± 0.288)
	W																							1.217 (± 0.343)
b) Spiders	Richness																							
	S																							403.430 (± 0.560)
	SB																							403.430 (± 2.204)
	G				- *					- *		+ ns		- **				+ *			- *			+ **	34.966 (± 24.308)
	H										- *		- *	+ **	- **										1.844 (± 0.422)
	NH		- ns									+ *		+ **	- ns										7.436 (± 2.655)
	W																								8.696 (± 2.945)
	Abundance																							
	S																							5.444 (± 1.225)
	SB																							7.563 (± 2.281)
	G						- *							- **	+ *									4.261 (± 0.874)
	H											- *		+ **	-**									0.904 (± 0.156)
	NH		- ns	- **	+ **					+ ns		+ ***		+ **		+ **	+ ***	- *			- ***		- ***		2.675 (± 0.541)
	W																								2.601 (± 0.523)

			Random effects	Fixed effects														Neg. binomial parameter
			Farm	**N**	**N *qf***	**Fo**	**Fo *qf***	**"L"**	**"M"**	**"Hi"**	**H[1]**	**H[1] *qf***	**W**	**W *qf***	**G**	**G *qf***	**I4**	
c) Earthworms	**Richness**	S																403.430 (± 0.417)
		SB																403.430 (± 1.495)
		G																403.430 (± 0.355)
		H											+ ns	- ns				22.186 (± 121.730)
		NH									- *							403.430 (± 3.913)
		W																5.835 (± 3.211)
	Abundance	S		+ ***	- **								- **		- *			6.348 (± 1.481)
		SB																7.737 (± 3.379)
		G																4.033 (± 0.756)
		H											+ ns	- ns				0.368 (± 0.091)
		NH		+ *	- *						- ***				+ *			1.366 (± 0.325)
		W																0.705 (± 0.137)
d) Plants	**Richness**	S				- ***												70.537 (± 33.858)
		SB		- **											- ns		+ *	403.430 (± 1.401)
		G						- ***										11.373 (± 2.958)
		H											+ *					10.167 (± 2.424)
		NH				- ***	+ *				- *				+ **	- ***		17.211 (± 5.036)
		W																9.752 (± 2.815)

Legend

S	Stalden	N	N input	I1	N input * field operations
SB	Southern Bavaria	Fo	Field operations	I2	N input * H^1 of surrounding habitats
G	Gascony	"L"	"Low" intensively managed fields vs. "very low" intensively managed fields	I3	Field operations * H^1 of surrounding habitats
H	Homokhátság			I4	N input * grassland habitats in the surroundings
NH	Northern Hedmark	"M"	"Moderate" intensively managed fields vs. "very low" intensively managed fields	I5	N input * woody habitats in the surroundings
W	Wales			I6	Field operations * woody habitats in the surroundings
		"Hi"	"High" intensively managed fields vs. "very low" intensively managed fields	I7	Grassy habitats in the surroundings * woody habitats in the surroundings
				I8	Field operations * grassy habitats in the surroundings
		H^1	H^1 of surrounding habitats	I9	H^1 of surrounding habitats * grassy habitats in the surroundings
		W	Woody habitats in the surroundings		
		G	Grassland habitats in the surroundings		
		qf	quadratic function		

[1] H = Shannon diversity index

Appendix D

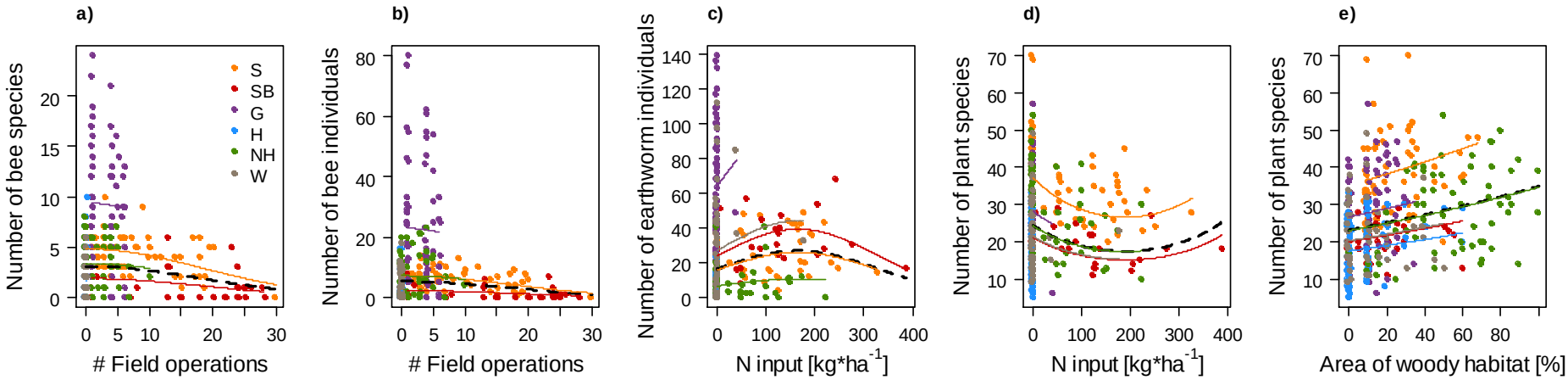

Fig. S1: Significant relationships between number of field operations per year (a) and (b), nitrogen input (c) and (d) and area of woody habitat (e), and species richness of bees (a), and plants (d) and (e), and abundance of bees (b) and earthworms (c) in 357 European grassland fields. Black, dashed lines indicate predicted values of best-fit binomial generalized mixed-effects models over all regions, colours indicate the six regions (S = Stalden, SB = Southern Bavaria, G = Gascony, H = Homokhátság, NH = Northern Hedmark and W = Wales).

Comment to (d)

The U-shaped curve resulting of the model was unexpected. Statistically, it was appropriate to be evaluated as the "best" model. However, to interpret it ecologically, the information that a second model, including random slopes for nitrogen input in regions, fitted the data well also (but not significantly better), needs to be considered.

Appendix E

Analysis for correlations between taxonomic groups

Introduction

The four taxonomic groups, bees, spiders, earthworms and plants, were selected due to their different needs and ecological functions. Therefore few correlations between the taxonomic groups were expected. However, if taxonomic groups are correlated, one could indicate presence and/or abundance of the other(s). We used the data of this study to investigate if the four taxonomic groups were correlated.

Methods

Procrustes rotation (Legendre and Legendre, 2012) for species compositions and Spearman rank correlation coefficients for species richness and abundance were employed. For each region and community aspect separately, we tested correlation between the four taxonomic groups, based on untransformed species data.

Results

Correlations among the four taxonomic groups were rare and differed among regions. Most significant correlations were found between bees and plants, and between spiders and earthworms. Bees and plants were correlated for species composition and species richness in three regions. Spider and earthworm species richness were negatively correlated in one region and positively correlated in two other regions. Spider and earthworm abundance were positively correlated in three regions (Table S10).

Table S6: Range of Procrustes rotation parameter (species composition) and pairwise Spearman's rank correlations (species richness and abundance) between the four taxonomic groups in the six regions. ρ = Spearman's rho. Regions where coefficients were significant are given as S = Stalden, SB = Southern Bavaria, G = Gascony, H = Homokhátság, NH = Northern Hedmark, W = Wales. Signs (+ and –) indicate positive and negative correlations.

	Composition		**Richness**		**Abundance**	
	Correlation in a symmetric Pro-crustes rotation	Regions where significant	ρ	Regions where significant	ρ	Regions where significant
Bees vs. Spiders	0.31 - 0.44	N	-0.16 - 0	-	-0.11 - 0	-
Bees vs. Earthworms	0.19 - 0.33	-	-0.22 - 0.32	W (+)	0 - 0.28	-
Spiders vs. Earthworms	0.24 - 0.37	-	- 0.42 - 0.46	W (-), H, NH (+)	-0.27 - 0.51	SB, H, NH (+)
Bees vs. Plants	0.37 - 0.52	S, G, W	0 - 0.44	G, H, W (+)	not tested	
Spiders vs. Plants	0.47 - 0.57	S, H, NH, W	0.16 – 0.25	-		
Earthworms vs. Plants	0.26 - 0.43	S, G, W	-0.28 - 0.37	S (-), W (+)		

Discussion

Significant correlations between bees and plants expressed the direct dependency of bees on plants as food resources (Steffan-Dewenter and Tscharntke, 2001). Significant correlations between spiders and earthworms could be explained by the plant litter covering the soil. Such litter provides food resource for earthworms and for other detritivores, which might be prey of spiders (Purvis and Curry, 1984).

Appendix F

Table S7: List of bee species. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and then alphabetically.

Bee species	Stalden	Southern Bavaria	Gascony	Homok-hátság	Northern Hedmark	Wales
Bombus pascuorum	44	5	25	1	34	16
Bombus terrestris gr.	12	4	19	5	25	20
Bombus hortorum	14	0	2	0	5	7
Bombus lapidarius	16	5	18	0	0	17
Bombus pratorum	3	0	2	0	30	5
Andrena subopaca	2	1	0	0	1	0
Bombus humilis	4	0	1	1	0	0
Bombus hypnorum	1	0	1	0	14	0
Bombus ruderatus	0	0	2	1	0	3
Bombus sylvarum	0	3	8	5	0	0
Dasypoda altercator	0	1	5	4	0	0
Eucera longicornis	2	3	7	0	0	0
Eucera nigrescens	8	0	6	3	0	0
Halictus rubicundus	2	1	0	0	1	0
Halictus tumulorum	10	0	8	1	0	0
Lasioglossum calceatum	18	3	2	0	0	0
Lasioglossum leucozonium	6	0	9	4	0	0
Lasioglossum pauxillum	4	1	17	0	0	0
Lasioglossum villosulum	2	0	13	1	0	0
Lasioglossum zonulum	22	0	5	1	0	0
Andrena chrysopyga	4	1	0	0	0	0
Andrena flavipes	0	2	11	0	0	0
Andrena gravida	4	1	0	0	0	0
Andrena haemorrhoa	11	2	0	0	0	0
Andrena minutula	0	1	1	0	0	0
Andrena ovatula	0	1	0	4	0	0
Andrena wilkella	4	0	1	0	0	0
Anthidiellum strigatum	0	1	1	0	0	0
Bombus bohemicus	6	0	0	0	7	0
Bombus jonellus	0	0	0	0	32	1
Bombus monticola	0	0	0	0	2	7
Bombus soroeensis	2	0	0	0	2	0
Bombus sp.	13	0	0	0	0	18
Bombus sylvestris	3	0	0	0	5	0
Ceratina cyanea	0	0	3	2	0	0
Halictus maculatus	0	0	18	1	0	0
Halictus quadricinctus	0	0	7	7	0	0
Halictus simplex	25	0	33	0	0	0
Halictus subauratus	0	0	7	2	0	0
Halictus vestitus	0	0	1	1	0	0
Heriades crenulatus	0	0	6	1	0	0
Heriades truncorum	0	0	5	1	0	0
Hoplitis leucomelana	0	0	1	1	0	0
Hylaeus gibbus	0	0	1	1	0	0
Lasioglossum albipes	0	0	4	5	0	0

Lasioglossum discum	0	0	5	4	0	0
Lasioglossum fulvicorne	0	0	1	1	0	0
Lasioglossum glabriusculum	0	0	15	1	0	0
Lasioglossum malachurum	10	0	37	0	0	0
Lasioglossum morio	1	0	3	0	0	0
Lasioglossum punctatissimum	0	0	2	1	0	0
Megachile apicalis	0	0	3	1	0	0
Megachile centuncularis	0	0	1	2	0	0
Megachile leachella	0	0	10	4	0	0
Megachile willughbiella	2	0	2	0	0	0
Nomada striata	1	1	0	0	0	0
Osmia caerulescens	0	0	1	2	0	0
Sphecodes ferruginatus	1	0	1	0	0	0
Andrena aeneiventris	0	0	1	0	0	0
Andrena alfkenella	0	0	1	0	0	0
Andrena carantonica	1	0	0	0	0	0
Andrena cineraria	2	0	0	0	0	0
Andrena fucata	0	0	0	0	1	0
Andrena fulvago	1	0	0	0	0	0
Andrena fulvata	1	0	0	0	0	0
Andrena hedikae	0	0	1	0	0	0
Andrena integra	0	0	0	1	0	0
Andrena labialis	0	0	10	0	0	0
Andrena labiata	2	0	0	0	0	0
Andrena limata	0	0	0	1	0	0
Andrena marginata	0	0	0	1	0	0
Andrena nana	0	0	1	0	0	0
Andrena nasuta	0	0	0	1	0	0
Andrena nitida	2	0	0	0	0	0
Andrena ranunculi	0	0	1	0	0	0
Andrena sp.	0	0	0	1	0	0
Andrena variabilis	0	0	1	0	0	0
Andrena ventricosa	0	0	14	0	0	0
Anthidium florentinum	0	0	0	1	0	0
Anthidium manicatum	0	0	5	0	0	0
Anthidium oblongatum	0	0	3	0	0	0
Anthophora bimaculata	0	0	0	4	0	0
Anthophora crinipes	0	0	0	1	0	0
Anthophora larvata	0	0	0	1	0	0
Anthophora plagiata	0	0	0	1	0	0
Anthophora plumipes	1	0	0	0	0	0
Anthophora pubescens	0	0	1	0	0	0
Bombus balteatus	0	0	0	0	1	0
Bombus barbutellus	1	0	0	0	0	0
Bombus cingulatus	0	0	0	0	4	0
Bombus confusus	0	0	1	0	0	0
Bombus consobrinus	0	0	0	0	13	0
Bombus flavidus	0	0	0	0	3	0
Bombus quadricolor	0	1	0	0	0	0
Bombus rupestris	1	0	0	0	0	0

Bombus sporadicus	0	0	0	0	4	0
Bombus wurflenii	0	0	0	0	22	0
Ceratina chalybea	0	0	2	0	0	0
Ceratina cucurbitina	0	0	5	0	0	0
Chelostoma florisomne	1	0	0	0	0	0
Coelioxys afra	0	0	4	0	0	0
Colletes daviesanus	0	0	0	1	0	0
Colletes fodiens	0	0	0	1	0	0
Colletes pallescens	0	0	0	1	0	0
Colletes similis	0	0	0	1	0	0
Dasypoda suripes	0	0	0	1	0	0
Eucera chrysopyga	0	0	0	6	0	0
Eucera clypeata	0	0	14	0	0	0
Eucera nigrifacies	0	0	6	0	0	0
Eucera sp.	0	0	1	0	0	0
Eucera taurica	0	0	8	0	0	0
Halictus asperulus	0	0	0	1	0	0
Halictus compressus	0	0	5	0	0	0
Halictus confusus	0	0	0	3	0	0
Halictus scabiosae	0	0	23	0	0	0
Halictus seladonius	0	0	0	1	0	0
Halictus semitectus	0	0	0	3	0	0
Halictus sexcinctus	0	0	0	3	0	0
Halictus smaragdulus	0	0	16	0	0	0
Halictus tetrazonius gr	0	0	0	6	0	0
Hoplitis tridentata	0	0	3	0	0	0
Hylaeus brevicornis	0	0	6	0	0	0
Hylaeus clypearis	0	0	3	0	0	0
Hylaeus confusus	0	0	1	0	0	0
Hylaeus difformis	0	0	1	0	0	0
Hylaeus euryscapus	0	0	3	0	0	0
Hylaeus gredleri	0	0	1	0	0	0
Hylaeus hyalinatus	0	0	2	0	0	0
Hylaeus leptocephalus	0	0	0	1	0	0
Hylaeus nigritus	0	0	2	0	0	0
Hylaeus pectoralis	0	0	0	1	0	0
Hylaeus pictipes	0	0	1	0	0	0
Hylaeus sp.	0	0	2	0	0	0
Hylaeus trinotatus	0	0	0	1	0	0
Hylaeus tyrolensis	0	0	1	0	0	0
Hylaeus variegatus	0	0	3	0	0	0
Lasioglossum bluethgeni	0	0	0	1	0	0
Lasioglossum boreale	0	0	0	0	1	0
Lasioglossum brevicorne	0	0	0	1	0	0
Lasioglossum clypeare	0	0	0	2	0	0
Lasioglossum convexiusculum	0	0	0	2	0	0
Lasioglossum corvinum	0	0	10	0	0	0
Lasioglossum interruptum	0	0	14	0	0	0
Lasioglossum laevigatum	1	0	0	0	0	0

Lasioglossum laticeps	2	0	0	0	0	0
Lasioglossum lativentre	0	0	3	0	0	0
Lasioglossum leucopus	0	0	0	0	1	0
Lasioglossum lucidulum	0	0	0	1	0	0
Lasioglossum majus	0	0	1	0	0	0
Lasioglossum mesosclerum	0	0	0	1	0	0
Lasioglossum minutissimum	0	0	1	0	0	0
Lasioglossum politum	0	0	19	0	0	0
Lasioglossum puncticolle	0	0	7	0	0	0
Lasioglossum pygmaeum	0	0	1	0	0	0
Lasioglossum quadrinotatum	0	1	0	0	0	0
Lasioglossum semilucens	0	0	1	0	0	0
Lasioglossum sp.	0	0	5	0	0	0
Lasioglossum subhirtum	0	0	1	0	0	0
Lasioglossum xanthopum	0	0	0	2	0	0
Lithurgus chrysurus	0	0	6	0	0	0
Lithurgus cornutus	0	0	4	0	0	0
Megachile circumcincta	0	0	0	5	0	0
Megachile ericetorum	1	0	0	0	0	0
Megachile maritima	0	0	1	0	0	0
Megachile melanopyga	0	0	1	0	0	0
Megachile pilidens	0	0	1	0	0	0
Megachile rotundata	0	0	2	0	0	0
Melitta leporina	0	0	2	0	0	0
Melitta tricincta	0	0	1	0	0	0
Nomada basalis	0	0	1	0	0	0
Nomada distinguenda	0	0	2	0	0	0
Nomada fucata	0	0	2	0	0	0
Nomada furva	0	0	1	0	0	0
Nomada goodeniana	1	0	0	0	0	0
Nomada integra	1	0	0	0	0	0
Nomada kholi	0	0	3	0	0	0
Nomia diversipes	0	0	0	3	0	0
Nomia ruficornis	0	0	0	1	0	0
Osmia aurulenta	0	0	0	3	0	0
Osmia gallarum	0	0	1	0	0	0
Osmia rufa	3	0	0	0	0	0
Osmia rufohirta	0	0	1	0	0	0
Osmia xanthomelana	2	0	0	0	0	0
Panurgus dentipes	0	0	3	0	0	0
Pasites maculatus	0	0	0	1	0	0
Rophites algirus	0	0	1	0	0	0
Rophites hartmanni	0	0	0	1	0	0
Sphecodes alternatus	0	0	0	1	0	0
Sphecodes crassus	1	0	0	0	0	0
Sphecodes ephippius	0	0	1	0	0	0

Sphecodes longulus	0	0	2	0	0	0
Sphecodes monilicornis	0	0	1	0	0	0
Sphecodes puncticeps	0	0	1	0	0	0
Sphecodes scabricollis	1	0	0	0	0	0
Stelis annulata	0	0	1	0	0	0
Stelis phaeoptera	0	0	0	1	0	0
Tetralonia malvae	0	0	1	0	0	0
Tetralonia pollinosa	0	0	0	1	0	0
Tetralonia ruficornis	0	0	0	1	0	0
Tetralonia salicariae	0	0	0	3	0	0
Tetraloniella alticincta	0	0	2	0	0	0
Tetraloniella nana	0	0	0	1	0	0
Thyreus histrionicus	0	0	0	1	0	0
Trachusa byssinum	1	0	0	0	0	0
Trachusa interrupta	0	0	1	0	0	0
Xylocopa iris	0	0	1	0	0	0
Xylocopa valga	0	0	1	0	0	0
Xylocopa violacea	0	0	3	0	0	0

Table S8: List of spider species. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and then alphabetically.

Spider species	**Stalden**	**Southern Bavaria**	**Gascony**	**Homok-hátság**	**Northern Hedmark**	**Wales**
Erigone dentipalpis	30	26	1	12	11	23
Pardosa palustris	12	11	1	3	3	1
Bathyphantes gracilis	0	4	2	1	9	21
Centromerita bicolor	1	8	3	0	16	25
Dicymbium nigrum	20	19	5	0	4	32
Hahnia nava	7	0	24	1	1	1
Meioneta rurestris	10	23	34	34	1	0
Micrargus herbigradus	2	1	1	0	3	19
Microlinyphia pusilla	0	2	2	2	6	2
Ozyptila trux	0	1	1	1	1	3
Pachygnatha degeeri	57	31	32	17	0	33
Pirata latitans	3	1	4	2	0	3
Xysticus cristatus	1	0	2	2	4	10
Centromerus sylvaticus	1	0	4	0	3	2
Ceratinella brevipes	11	1	0	0	7	17
Ceratinella brevis	0	2	6	1	0	3
Cnephalocotes obscurus	17	0	11	0	4	8
Diplostyla concolor	1	4	17	2	0	0
Enoplognatha thoracica	11	1	3	1	0	0
Erigone atra	6	29	0	0	30	30
Maso sundevalli	1	0	7	0	4	3
Microneta viaria	0	0	2	1	1	2
Neottiura bimaculata	0	8	7	10	0	2
Oedothorax apicatus	2	11	6	1	0	0
Ozyptila atomaria	4	0	0	2	1	3
Pachygnatha clercki	0	5	1	1	0	10
Pardosa prativaga	0	2	6	5	3	0
Pardosa pullata	10	1	6	0	0	14
Pelecopsis parallela	2	3	6	0	0	8

Phrurolithus festivus	1	1	11	4	0	0
Pocadicnemis juncea	0	1	3	4	0	3
Pocadicnemis pumila	1	1	0	0	3	8
Tenuiphantes tenuis	2	17	44	3	0	0
Tibellus oblongus	0	0	1	2	1	2
Tiso vagans	41	17	0	0	4	18
Xysticus kochi	1	1	5	2	0	0
Zora spinimana	0	1	9	3	1	0
Alopecosa pulverulenta	9	0	2	0	1	0
Araneus diadematus	1	0	0	4	0	4
Araneus quadratus	0	1	0	1	0	4
Clubiona reclusa	0	0	1	0	2	1
Diplocephalus latifrons	1	2	0	0	2	0
Enoplognatha ovata	2	0	1	0	0	3
Erigonella hiemalis	0	3	0	0	18	11
Ero furcata	1	0	7	0	0	1
Euophrys frontalis	12	0	25	8	0	0
Evarcha arcuata	0	1	7	8	0	0
Heliophanus cupreus	4	0	3	1	0	0
Heliophanus flavipes	12	0	8	9	0	0
Hypsosinga sanguinea	2	0	1	5	0	0
Kaestneria pullata	0	0	0	1	3	2
Linyphia triangularis	2	0	1	2	0	0
Mermessus trilobatus	56	20	5	0	0	0
Micaria pulicaria	1	0	1	0	1	0
Neriene clathrata	0	1	5	0	0	4
Oedothorax fuscus	14	19	0	0	0	30
Oedothorax retusus	1	0	0	0	30	23
Phlegra fasciata	2	0	1	1	0	0
Pirata piraticus	0	0	0	1	2	5
Pisaura mirabilis	0	0	5	21	0	1
Robertus arundineti	0	0	1	1	0	2
Robertus lividus	0	0	1	0	3	2
Robertus neglectus	2	2	0	0	2	0
Sibianor aurocinctus	0	0	6	1	1	0
Talavera aequipes	1	0	5	7	0	0
Tenuiphantes flavipes	1	0	3	1	0	0
Walckenaeria antica	8	0	0	0	2	10
Xysticus erraticus	3	0	16	0	0	9
Araeoncus humilis	0	21	0	4	0	0
Argenna subnigra	0	0	8	3	0	0
Argiope bruennichi	0	0	13	13	0	0
Aulonia albimana	0	0	22	5	0	0
Bathyphantes nigrinus	0	2	0	0	5	0
Bolyphantes luteolus	0	0	0	0	1	6
Centromerus dilutus	0	0	1	0	0	8
Clubiona diversa	0	0	0	6	0	2
Clubiona pseudoneglecta	0	0	8	1	0	0
Clubiona terrestris	1	0	1	0	0	0
Collinsia inerrans	9	0	0	0	2	0
Crustulina guttata	1	0	4	0	0	0
Dicymbium tibiale	0	0	0	0	36	2

Dismodicus bifrons	0	1	0	0	8	0
Drassodes pubescens	0	0	1	2	0	0
Drassyllus lutetianus	0	1	0	1	0	0
Drassyllus praeficus	0	0	6	1	0	0
Erigone capra	0	0	0	0	3	1
Gnathonarium dentatum	0	0	0	2	0	3
Gonatium rubens	0	0	0	0	2	8
Gongylidiellum murcidum	3	1	0	0	0	0
Gongylidiellum vivum	0	0	2	0	0	21
Hahnia montana	0	0	1	0	0	4
Hilaira excisa	0	0	0	0	8	3
Hypsosinga pygmaea	0	0	3	3	0	0
Leptorhoptrum robustum	0	0	0	0	28	2
Lophomma punctatum	0	0	0	0	3	7
Mangora acalypha	0	0	2	3	0	0
Marpissa nivoyi	0	0	4	2	0	0
Maso gallicus	0	0	1	0	0	2
Meioneta affinis	0	0	0	2	7	0
Meioneta mollis	0	0	26	4	0	0
Meioneta simplicitarsis	0	0	2	12	0	0
Metellina segmentata	1	0	0	0	0	6
Micrargus subaequalis	0	0	10	0	0	1
Minyriolus pusillus	0	0	1	0	1	0
Misumena vatia	0	0	1	3	0	0
Monocephalus fuscipes	1	0	0	0	0	2
Myrmarachne formicaria	0	0	3	1	0	0
Ozyptila praticola	0	0	2	1	0	0
Ozyptila sanctuaria	0	0	2	0	0	1
Ozyptila scabricula	0	0	1	1	0	0
Ozyptila simplex	2	0	15	0	0	0
Panamomops sulcifrons	1	0	12	0	0	0
Pardosa amentata	2	0	0	0	7	0
Pardosa hortensis	0	0	3	0	0	1
Pardosa nigriceps	0	0	1	0	0	2
Pardosa saltans	3	0	1	0	0	0
Philodromus pulchellus	0	0	3	1	0	0
Phylloneta impressa	1	0	0	5	0	0
Porrhomma microphthalmum	0	2	4	0	0	0
Porrhomma pallidum	0	0	0	0	1	1
Runcinia grammica	0	0	2	12	0	0
Savignia frontata	0	0	0	0	30	19
Tenuiphantes tenebricola	0	0	0	1	5	0
Tetragnatha extensa	0	0	1	2	0	0
Tetragnatha pinicola	1	2	0	0	0	0
Tibellus macellus	0	0	1	7	0	0
Trichoncus hackmani	0	0	1	10	0	0
Trichopterna cito	0	0	0	4	0	1
Trochosa terricola	5	0	0	0	0	2

Walckenaeria acuminata	0	0	1	0	0	4
Walckenaeria alticeps	0	0	1	1	0	0
Walckenaeria atrotibialis	1	0	1	0	0	0
Walckenaeria kochi	0	0	0	0	2	1
Walckenaeria unicornis	0	0	0	1	0	2
Xerolycosa miniata	0	0	1	1	0	0
Xysticus audax	0	1	0	1	0	0
Xysticus ninnii	1	0	0	1	0	0
Zelotes latreillei	0	0	1	0	0	1
Acartauchenius scurrilis	0	0	0	2	0	0
Aelurillus v-insignitus	0	0	0	2	0	0
Agalenatea redii	0	0	0	1	0	0
Agnyphantes expunctus	0	0	0	0	1	0
Agraecina lineata	0	0	6	0	0	0
Agroeca lusatica	0	0	2	0	0	0
Agroeca proxima	0	0	0	0	0	1
Agyneta cauta	0	0	0	0	1	0
Agyneta conigera	0	0	0	0	0	1
Agyneta decora	0	0	0	0	0	3
Allagelena gracilens	0	0	1	0	0	0
Allomengea scopigera	0	0	0	0	26	0
Antistea elegans	0	0	0	0	0	1
Aphileta misera	0	0	0	0	0	5
Araniella displicata	1	0	0	0	0	0
Arctosa leopardus	1	0	0	0	0	0
Arctosa lutetiana	0	0	0	1	0	0
Asthenargus paganus	0	0	0	0	3	0
Bathyphantes approximatus	0	0	0	0	0	3
Bathyphantes parvulus	0	0	0	0	0	1
Bathyphantes similis	0	0	0	8	0	0
Bathyphantes sp.	0	0	1	0	0	0
Bolyphantes alticeps	0	0	0	0	25	0
Centromerita concinna	0	0	0	0	0	17
Centromerus arcanus	0	0	0	0	3	0
Centromerus incilium	0	0	0	0	1	0
Centromerus minutissimus	0	0	2	0	0	0
Centromerus sp.	0	0	2	0	0	0
Ceratinella scabrosa	1	0	0	0	0	0
Cercidia prominens	0	0	1	0	0	0
Cheiracanthium mildei	0	0	0	1	0	0
Cheiracanthium pennyi	0	0	0	3	0	0
Cheiracanthum sp.	0	0	1	0	0	0
Clubiona neglecta	3	0	0	0	0	0
Clubiona phragmitis	0	0	0	1	0	0
Clubiona rosserae	0	0	0	1	0	0
Clubiona subsultans	0	0	0	0	1	0
Clubiona subtilis	0	0	0	7	0	0
Collinsia sp.	0	0	2	0	0	0
Cozyptila blackwalli	0	0	2	0	0	0

Cresmatoneta mutinensis	0	0	7	0	0	0
Crustulina sticta	0	0	2	0	0	0
Cryphoeca silvicola	0	0	0	0	5	0
Diaea dorsata	1	0	0	0	0	0
Dictyna arundinacea	0	0	0	10	0	0
Dictyna latens	0	0	1	0	0	0
Dictyna pusilla	1	0	0	0	0	0
Diplocentria bidentata	0	0	0	0	9	0
Diplocephalus cristatus	0	2	0	0	0	0
Diplocephalus permixtus	0	0	0	0	0	7
Diplocephalus picinus	0	0	1	0	0	0
Drassyllus pusillus	0	0	1	0	0	0
Drassyllus villicus	0	0	1	0	0	0
Drepanotylus uncatus	0	0	0	0	0	1
Ebrechtella tricuspidata	0	0	0	10	0	0
Emblyna brevidens	0	0	0	1	0	0
Enoplognatha latimana	0	0	2	0	0	0
Enoplognatha mordax	0	0	0	1	0	0
Enoplognatha oelandica	0	0	0	1	0	0
Entelecara flavipes	0	0	4	0	0	0
Episinus truncatus	0	0	9	0	0	0
Erigonella ignobilis	0	0	0	0	0	10
Ero aphana	0	0	1	0	0	0
Ero cambridgei	0	0	0	0	0	4
Euophrys gambosa	0	0	4	0	0	0
Euryopis flavomaculata	0	0	3	0	0	0
Euryopis quinqueguttata	0	0	1	0	0	0
Euryopis saukea	0	0	0	1	0	0
Evarcha falcata	0	0	0	2	0	0
Gonatium paradoxum	0	0	0	0	1	0
Gonatium rubellum	0	0	0	0	8	0
Gongylidiellum latebricola	3	0	0	0	0	0
Hahnia pusilla	0	1	0	0	0	0
Hahnia sp.	0	0	2	0	0	0
Haplodrassus minor	0	0	0	2	0	0
Helophora insignis	0	0	0	0	4	0
Hilaira herniosa	0	0	0	0	1	0
Hilaira pervicax	0	0	0	0	6	0
Hygrolycosa rubrofasciata	0	0	0	0	1	0
Hypomma bituberculatum	0	0	0	0	5	0
Hypsosinga heri	0	0	0	2	0	0
Larinioides sclopetarius	0	0	0	1	0	0
Larinioides suspicax	0	0	0	7	0	0
Lasiargus hirsutus	0	0	7	0	0	0
Lathys humilis	1	0	0	0	0	0
Latithorax faustus	0	0	0	0	0	7
Lepthyphantes cristatus	0	0	0	0	0	2
Lepthyphantes ericaeus	0	0	0	0	0	28

Lepthyphantes mengei	0	0	0	0	0	21
Lepthyphantes tenuis	0	0	0	0	0	29
Lepthyphantes zimmermanni	0	0	0	0	0	5
Leptodrassus albidus	0	0	1	0	0	0
Linyphiidae	0	0	5	0	0	0
Liocranoeca striata	0	0	0	1	0	0
Macrargus carpenteri	0	0	0	0	1	0
Macrargus rufus	0	0	0	0	2	0
Meioneta saxatilis	0	0	0	0	0	5
Mendoza canestrinii	0	0	0	2	0	0
Meta segmentata	0	0	0	0	1	0
Metellina mengei	1	0	0	0	0	0
Metopobactrus prominulus	0	0	3	0	0	0
Micaria dives	0	0	0	1	0	0
Micaria guttulata	0	0	1	0	0	0
Micaria romana	0	0	0	1	0	0
Microlinyphia impigra	0	0	0	1	0	0
Micrommata ligurina	0	0	1	0	0	0
Micrommata virescens	0	0	0	5	0	0
Milleriana inerrans	0	0	0	0	0	2
Minicia marginella	0	0	0	0	3	0
Mysmenella jobi	0	0	0	2	0	0
Neon reticulatus	0	0	0	1	0	0
Neon valentulus	0	0	0	2	0	0
Neoscona adianta	0	0	0	1	0	0
Neottiura suaveolens	0	0	0	1	0	0
Neriene emphana	0	0	0	1	0	0
Neriene furtiva	0	0	6	0	0	0
Nomisia exornata	0	0	2	0	0	0
Nusoncus nasutus	1	0	0	0	0	0
Oedothorax gibbosus	0	0	0	0	0	5
Oreoneta frigida	0	0	0	0	2	0
Oryphantes angulatus	0	0	0	0	24	0
Oxyopes heterophthalmus	0	0	0	3	0	0
Oxyopes lineatus	0	0	5	0	0	0
Ozyptila sp.	0	0	1	0	0	0
Palliduphantes alutacius	0	0	1	0	0	0
Palliduphantes pallidus	0	1	0	0	0	0
Pardosa agrestis	0	0	0	2	0	0
Pardosa agricola	0	0	0	0	1	0
Pardosa alacris	0	0	0	1	0	0
Pardosa cribrata	0	0	0	2	0	0
Pardosa fulvipes	0	0	0	0	2	0
Pardosa lugubris	0	0	0	0	3	0
Pardosa paludicola	0	0	0	1	0	0
Pardosa proxima	0	0	8	0	0	0
Pardosa riparia	0	0	0	0	6	0
Pardosa sphagnicola	0	0	0	0	3	0
Pelecopsis bucephala	0	0	1	0	0	0
Pelecopsis mengei	0	0	0	0	0	1

Peponocranium ludicrum	0	0	0	0	0	7
Philaeus chrysops	0	0	0	1	0	0
Philodromus albidus	0	0	0	1	0	0
Philodromus cespitum	0	0	0	1	0	0
Philodromus dispar	0	0	1	0	0	0
Phlegra bresnieri	0	0	2	0	0	0
Pholcomma gibbum	0	0	0	0	0	4
Phrurolithus minimus	0	0	0	1	0	0
Phrurolithus nigrinus	0	0	6	0	0	0
Pirata piscatorius	0	0	0	0	0	1
Platnickina tincta	0	1	0	0	0	0
Poeciloneta globosa	0	0	0	0	0	1
Porrhomma errans	0	0	0	0	0	1
Porrhomma pygmaeum	0	0	0	0	0	2
Prinerigone vagans	0	0	0	1	0	0
Robertus scoticus	0	0	0	0	1	0
Saaristoa abnormis	0	0	0	0	0	1
Saitis barbipes	0	0	3	0	0	0
Scotina celans	0	0	1	0	0	0
Semljicola faustus	0	0	0	0	5	0
Semljicola latus	0	0	0	0	19	0
Setaphis carmeli	0	0	2	0	0	0
Silometopus elegans	0	0	0	0	0	1
Silometopus reussi	0	0	0	1	0	0
Singa hamata	0	0	0	6	0	0
Singa nitidula	0	0	0	1	0	0
Sitticus rupicola	0	0	0	1	0	0
Styloctetor romanus	0	0	0	2	0	0
Synema globosum	0	0	0	1	0	0
Talavera inopinata	0	0	2	0	0	0
Tallusia experta	0	0	0	0	0	4
Tapinocyba insecta	2	0	0	0	0	0
Tapinocyba pallens	0	0	0	0	0	1
Tapinocyba praecox	0	0	0	0	0	2
Tapinopa longidens	0	0	0	0	0	2
Taranucnus setosus	0	0	0	0	0	1
Tenuiphantes alacris	0	0	0	0	4	0
Tenuiphantes mengei	0	0	0	0	19	0
Tenuiphantes nigriventris	0	0	0	0	3	0
Tetragnatha obtusa	1	0	0	0	0	0
Thanatus arenarius	0	0	0	2	0	0
Thanatus atratus	0	0	7	0	0	0
Theonoe minutissima	0	0	0	0	0	2
Theridion boesenbergi	0	1	0	0	0	0
Theridion impressum	0	0	7	0	0	0
Theridion sisyphium	0	0	0	0	0	1
Theridion uhligi	0	0	0	2	0	0
Thomisus onustus	0	0	0	4	0	0
Titanoeca quadriguttata	0	0	0	1	0	0
Titanoeca tristis	0	0	1	0	0	0
Tmarus piger	0	0	0	1	0	0

Trachelas minor	0	0	21	0	0	0
Trachyzelotes fuscipes	0	0	1	0	0	0
Trachyzelotes pedestris	0	0	3	0	0	0
Trichoncus affinis	0	0	0	12	0	0
Trichoncus saxicola	0	0	12	0	0	0
Trochosa hispanica	0	0	1	0	0	0
Trochosa ruricola	0	2	0	0	0	0
Trochosa spinipalpis	0	0	0	0	2	0
Walckenaeria cuspidata	0	0	0	0	1	0
Walckenaeria dysderoides	1	0	0	0	0	0
Walckenaeria nodosa	0	0	0	0	0	1
Walckenaeria nudipalpis	0	0	0	0	0	1
Walckenaeria obtusa	0	0	0	0	2	0
Walckenaeria vigilax	0	0	0	0	0	2
Xysticus bifasciatus	7	0	0	0	0	0
Xysticus lanio	0	0	1	0	0	0
Xysticus sp.	0	0	2	0	0	0
Zelotes atrocaeruleus	0	0	1	0	0	0
Zelotes civicus	0	0	20	0	0	0
Zelotes electus	0	0	0	3	0	0
Zelotes petrensis	0	0	1	0	0	0
Zelotes pygmaeus	0	0	0	1	0	0
Zodarion germanicum	0	0	0	1	0	0
Zodarion italicum	0	0	1	0	0	0
Zodarion rubidum	0	0	1	0	0	0
Zora armillata	0	0	0	15	0	0
Zora parallela	0	0	7	0	0	0
Zora pardalis	0	0	1	0	0	0
Zornella cultigera	0	0	0	0	2	0

Table S9: List of earthworm species. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and then alphabetically.

Earthworm species	Stalden	Southern Bavaria	Gascony	Homok-hátság	Northern Hedmark	Wales
Allolobophora caliginosa	58	30	59	13	32	34
Allolobophora rosea	58	29	34	27	11	24
Allolobophora chlorotica	10	5	51	1	0	30
Eiseniella tetraedra	2	1	1	0	3	2
Lumbricus castaneus	12	14	6	0	1	17
Lumbricus rubellus rubellus	47	19	0	4	29	30
Octolasium lacteum	30	10	6	0	4	2
Dendrobaena octaedra	8	0	2	0	36	2
Lumbricus terrestris	37	23	0	0	3	13
Octolasium cyaneum	40	9	15	0	0	18
Allolobophora georgii	0	1	0	11	0	0
Allolobophora longa	35	0	0	0	0	9
Allolobophora muldali	1	0	19	0	0	0
Dendrobaena mammalis	0	0	14	0	0	13
Dendrodrilus rubidus	0	0	0	0	13	6
Allolobophora cupulifera	0	0	2	0	0	0
Allolobophora icterica	13	0	0	0	0	0
Allolobophora jassyensis	0	0	0	1	0	0
Lumbricus eiseni	0	0	0	0	0	1
Lumbricus festivus	0	0	0	0	0	4
Lumbricus friendi	0	0	57	0	0	0
Lumbricus herculeus	0	0	5	0	0	0
Lumbricus sp.	0	0	0	0	0	1
Nicodrilus cuendeti	15	0	0	0	0	0
Nicodrilus nocturnus	5	0	0	0	0	0
Octodrilus transpadanum	0	2	0	0	0	0
Prosellodrilus fragilis	0	0	56	0	0	0
Scheroteca savignyi	0	0	43	0	0	0

Table S10: List of plant species. Numbers indicate the number of fields where the species occurred. Species are listed firstly according to their occurrence in number of regions and then alphabetically.

Plant species	Stalden	Southern Bavaria	Gascony	Homok-hátság	Northern Hedmark	Wales
Agrostis stolonifera	1	7	9	15	2	19
Alopecurus pratensis	23	21	1	10	18	3
Dactylis glomerata	56	27	48	35	14	14
Festuca pratensis	14	17	39	2	15	2
Festuca rubra	47	2	14	1	39	18
Myosotis arvensis	1	1	22	1	13	4
Poa pratensis	26	26	10	3	48	8

Poa trivialis	33	8	30	2	13	11
Ranunculus acris	63	21	18	10	45	15
Ranunculus repens	34	18	8	13	23	29
Rumex acetosa	57	14	18	2	43	27
Trifolium pratense	56	19	29	6	30	10
Trifolium repens	61	30	27	8	36	29
Urtica dioica	4	1	5	1	27	8
Achillea millefolium	28	15	5	0	43	11
Agrostis capillaris	27	9	9	0	50	38
Anthemis odorata	65	5	20	0	29	35
Cerastium fontanum	54	11	3	2	28	0
Equisetum arvense	5	1	6	1	8	0
Festuca arundinacea	1	1	14	18	0	2
Festuca ovina	2	1	9	0	2	36
Lathyrus pratensis	18	0	25	1	4	1
Lolium perenne	53	26	12	1	0	26
Phleum pratense	2	14	7	0	22	8
Plantago lanceolata	63	28	28	32	0	13
Plantago major	16	7	4	0	3	2
Prunella vulgaris	37	7	11	0	8	9
Rhinanthus minor	1	0	2	8	19	1
Stellaria media	13	0	2	13	8	7
Veronica chamaedrys	55	5	7	0	5	7
Veronica persica	1	1	8	1	0	1
Ajuga reptans	59	5	4	0	0	1
Angelica sylvestris	3	0	0	1	1	1
Anthriscus sylvestris	10	1	1	0	26	0
Arrhenatherum elatius	26	2	33	0	0	2
Bellis perennis	46	20	14	0	0	7
Briza media	1	0	8	2	0	2
Bromus hordeaceus	25	3	14	6	0	0
Calluna vulgaris	1	0	1	0	3	5
Caltha palustris	2	0	0	5	5	2
Capsella bursa-pastoris	10	2	0	15	2	0
Carex flacca	13	0	24	4	0	5
Carex panicea	3	0	0	3	3	3
Carex sp.	1	1	2	0	0	11
Centaurea jacea	3	1	32	12	0	0
Cynodon dactylon	4	11	4	0	0	25
Deschampsia cespitosa	1	0	0	15	50	7
Elymus repens	0	2	0	32	13	2
Equisetum palustre	2	0	0	1	5	1
Filipendula ulmaria	5	1	0	0	10	1
Fraxinus excelsior	5	0	1	1	0	2
Galium mollugo	39	7	14	0	7	0
Holcus lanatus	57	20	33	0	0	42
Hypochaeris radicata	32	1	11	0	0	7
Juncus effusus	4	1	0	2	0	17
Lamium purpureum	6	0	2	1	0	1
Leucanthemum vulgare	27	0	18	0	8	1
Lotus corniculatus	17	0	33	13	0	20
Poa annua	23	5	0	0	7	18
Potentilla erecta	9	0	0	3	10	22

Rumex acetosella	0	0	4	1	6	8
Rumex crispus	0	5	26	2	0	3
Taraxacum officinale	58	30	0	39	0	22
Veronica officinalis	5	0	4	0	3	3
Veronica serpyllifolia	29	7	0	0	18	6
Vicia cracca	10	0	4	4	15	0
Vicia sepium	27	1	1	0	6	0
Alchemilla vulgaris	46	4	0	0	0	1
Cardamine hirsuta	11	4	0	0	0	2
Cardamine pratensis	45	0	0	0	1	12
Carex hirta	4	0	7	1	0	0
Carex nigra	1	0	0	0	14	3
Carex ovalis	0	1	0	0	1	1
Carum carvi	3	12	0	0	4	0
Cirsium arvense	0	0	17	11	0	17
Cirsium palustre	2	0	0	0	2	24
Cirsium vulgare	0	0	2	1	0	7
Convolvulus arvensis	0	2	33	12	0	0
Crataegus monogyna	0	0	7	7	0	2
Daucus carota	9	0	32	12	0	0
Equisetum sylvaticum	1	0	0	0	1	1
Galium aparine	0	0	16	1	0	1
Galium palustre	0	0	0	5	1	7
Galium verum	0	0	6	30	0	2
Geranium dissectum	1	1	33	0	0	0
Heracleum sphondylium	26	10	0	0	0	1
Knautia arvensis	12	0	0	3	8	0
Leontodon autumnalis	1	8	0	0	17	0
Leontodon hispidus	19	0	0	3	0	4
Lolium multiflorum	37	24	15	0	0	0
Luzula campestris	35	0	4	0	0	3
Luzula multiflora	1	0	0	0	25	1
Medicago lupulina	18	0	12	15	0	0
Melampyrum pratense	1	0	0	0	2	1
Molinia caerulea	2	0	0	5	0	6
Nardus stricta	3	0	0	0	14	8
Picris hieracioides	1	0	2	4	0	0
Pimpinella saxifraga	2	0	0	9	0	3
Plantago media	4	0	0	2	0	2
Polygala vulgaris	6	0	3	0	0	4
Populus tremula	1	0	1	0	4	0
Potentilla reptans	7	0	41	16	0	0
Ranunculus bulbosus	6	0	23	0	0	3
Ranunculus ficaria	16	0	1	0	0	1
Rubus fruticosus	4	0	5	0	0	3
Rumex obtusifolius	42	18	0	0	0	8
Salix caprea	1	0	2	0	4	0
Senecio jacobaea	0	0	9	1	0	6
Senecio vulgaris	1	0	4	1	0	0
Silene vulgaris	6	0	0	11	11	0
Sonchus arvensis	0	0	3	3	0	1
Sorbus aucuparia	2	0	0	0	7	1
Stellaria graminea	1	0	3	0	28	0

Succisa pratensis	2	0	2	0	2	0
Taraxacum sp.	0	0	22	0	29	1
Trifolium campestre	8	0	9	5	0	0
Trifolium dubium	3	1	4	0	0	0
Trisetum flavescens	12	11	19	0	0	0
Vaccinium myrtillus	4	0	0	0	17	8
Vaccinium vitis-idaea	2	0	0	0	9	2
Veronica arvensis	28	0	2	27	0	0
Achillea ptarmica	0	0	0	0	13	2
Agrimonia eupatoria	0	0	15	1	0	0
Alchemilla glabra	1	0	0	0	8	0
Anthyllis vulneraria	1	0	0	1	0	0
Arctium lappa	0	0	2	2	0	0
Artemisia vulgaris	0	0	4	1	0	0
Brachypodium pinnatum	4	0	8	0	0	0
Brassica napus	0	1	2	0	0	0
Bromus erectus	8	0	11	0	0	0
Bromus ramosus	0	0	0	1	0	1
Bromus sterilis	0	0	15	5	0	0
Calystegia sepium	0	0	17	6	0	0
Campanula rotundifolia	0	0	0	0	4	3
Carduus nutans	0	0	25	17	0	0
Carex acutiformis	0	2	0	10	0	0
Carex caryophyllea	13	0	0	2	0	0
Carex demissa	0	0	0	0	2	5
Carex digitata	1	0	0	0	1	0
Carex divulsa	0	0	4	0	0	1
Carex echinata	0	0	0	0	2	5
Carex flava	1	0	0	0	2	0
Carex otrubae	0	0	1	2	0	0
Carex pallescens	5	0	0	0	9	0
Carex pilulifera	0	0	1	0	1	0
Carex tomentosa	1	0	0	1	0	0
Centaurea scabiosa	1	0	0	0	0	1
Centaurium erythraea	1	0	3	0	0	0
Chenopodium album	0	1	0	2	0	0
Chrysosplenium oppositifolium	0	1	0	0	0	1
Cirsium oleraceum	5	4	0	0	0	0
Clematis vitalba	1	0	4	0	0	0
Conyza canadensis	0	0	13	2	0	0
Crepis biennis	12	12	0	0	0	0
Crepis capillaris	0	1	0	0	0	7
Crepis vesicaria	1	0	2	0	0	0
Cruciata laevipes	1	0	6	0	0	0
Cynoglossum officinale	0	0	4	23	0	0
Deschampsia flexuosa	0	0	0	0	17	2
Epilobium palustre	0	0	0	0	6	5
Epilobium tetragonum	0	0	15	0	0	1
Equisetum telmateia	2	0	2	0	0	0
Erigeron annuus	1	0	0	1	0	0
Eryngium campestre	0	0	10	10	0	0
Eupatorium cannabinum	1	0	1	0	0	0

Fragaria vesca	16	0	0	0	1	0
Genista tinctoria	0	0	3	4	0	0
Geranium sylvaticum	1	0	0	0	35	0
Geum rivale	1	0	0	0	12	0
Glechoma hederacea	38	6	0	0	0	0
Glyceria fluitans	0	0	0	1	0	1
Hieracium lactucella	5	0	0	0	8	0
Hieracium murorum aggr.	3	0	0	0	5	0
Hieracium pilosella	3	0	5	0	0	0
Holcus mollis	0	1	0	0	0	4
Hypericum perforatum	2	0	21	0	0	0
Juglans regia	2	0	2	0	0	0
Juncus articulatus	0	0	0	0	2	2
Juncus inflexus	0	0	1	0	0	3
Juniperus communis	0	0	0	1	20	0
Lathyrus hirsutus	0	0	1	0	0	1
Lemna minor	0	0	0	3	0	1
Linum catharticum	2	0	0	0	0	1
Lychnis flos-cuculi	0	1	0	0	0	2
Lycopus europaeus	0	0	3	8	0	0
Lysimachia nemorum	16	0	0	0	0	1
Lythrum salicaria	0	0	1	3	0	0
Maianthemum bifolium	1	0	0	0	2	0
Malva neglecta	0	0	3	5	0	0
Medicago sativa	0	0	3	2	0	0
Mentha aquatica	0	0	0	10	0	1
Mentha arvensis	0	1	3	0	0	0
Montia fontana	0	0	0	0	3	1
Muscari comosum	0	0	2	1	0	0
Ononis spinosa	0	0	2	16	0	0
Ophrys apifera	1	0	3	0	0	0
Orchis mascula	1	0	0	0	0	1
Origanum vulgare	1	0	4	0	0	0
Oxalis acetosella	0	0	0	0	9	1
Papaver rhoeas	0	0	1	12	0	0
Phalaris arundinacea	0	1	0	6	0	0
Picea abies	3	0	0	0	3	0
Picris echioides	0	0	26	0	0	4
Pimpinella major	14	1	0	0	0	0
Poa angustifolia	0	1	0	54	0	0
Polygala amarella	1	0	0	8	0	0
Polygonum aviculare	0	0	0	3	3	0
Polygonum persicaria	0	0	1	0	0	1
Potentilla anserina	0	1	0	11	0	0
Potentilla sterilis	32	0	0	0	0	2
Primula veris	20	0	0	0	0	1
Prunus spinosa	1	0	9	0	0	0
Pteridium aquilinium	2	0	0	0	0	14
Pulicaria dysenterica	0	0	5	2	0	0
Quercus robur	0	1	8	0	0	0
Quercus sp.	4	0	0	0	0	1
Rosa canina	0	0	18	1	0	0

Rosa sp.	4	0	1	0	0	0
Rubus caesius	0	0	28	1	0	0
Salix repens	0	0	0	1	1	0
Salix sp.	2	0	0	0	0	1
Salvia pratensis	0	0	1	1	0	0
Sambucus nigra	1	0	0	3	0	0
Sanguisorba minor	4	0	15	0	0	0
Sanguisorba officinalis	0	3	0	5	0	0
Scirpus sylvaticus	1	1	0	0	0	0
Senecio erucifolius	0	0	1	4	0	0
Silene flos-cuculi	6	0	4	0	0	0
Silene nutans	0	0	1	2	0	0
Sinapis arvensis	0	0	2	0	0	1
Solidago virgaurea	2	0	0	0	17	0
Sonchus oleracea	4	0	1	0	0	0
Stachys officinalis	5	0	0	0	0	1
Stellaria holostea	0	0	1	0	0	1
Symphytum officinale	0	2	0	2	0	0
Tragopogon pratensis	1	0	18	0	0	0
Trifolium arvense	0	0	2	2	0	0
Trifolium hybridum	0	0	7	0	1	0
Trifolium medium	1	0	2	0	0	0
Trollius europaeus	1	0	0	0	10	0
Tussilago farfara	1	0	0	0	3	0
Ulmus minor	0	0	8	3	0	0
Valeriana dioica	2	0	0	0	0	1
Valeriana officinalis	1	0	1	0	0	0
Verbascum blattaria	0	0	1	6	0	0
Veronica filiformis	28	1	0	0	0	0
Vicia villosa	0	0	1	9	0	0
Viola canina	0	0	0	1	7	0
Viola odorata	1	0	0	1	0	0
Viola palustris	0	0	0	0	11	3
Viola sp.	3	0	1	0	0	0
Acer campestre	0	0	2	0	0	0
Acer negundo	0	0	0	1	0	0
Acer platanoides	1	0	0	0	0	0
Acer pseudoplatanus	0	0	1	0	0	0
Achillea aspleniifolia	0	0	0	5	0	0
Achillea collina	0	0	0	32	0	0
Achillea ochroleuca	0	0	0	1	0	0
Achillea pannonica	0	0	0	1	0	0
Achillea setacea	0	0	0	2	0	0
Aconitum vulparia	0	0	0	0	14	0
Adonis aestivalis	0	0	0	1	0	0
Adonis annua	0	0	1	0	0	0
Aegopodium podagraria	2	0	0	0	0	0
Agrostis canina	0	0	0	0	0	10
Agrostis gigantea	0	0	1	0	0	0
Ailanthus altissima	0	0	0	1	0	0
Ajuga chamaepitys	0	0	0	1	0	0
Alcea biennis	0	0	0	1	0	0
Alchemilla filicaulis	0	0	0	0	1	0

Alchemilla norvegica	0	0	0	0	4	0
Alchemilla subcrenata	0	0	0	0	35	0
Alchemilla wichurae	0	0	0	0	16	0
Alisma plantago-aquatica	0	0	0	1	0	0
Allium oleraceum	0	0	4	0	0	0
Allium schoenoprasum	0	0	4	0	0	0
Allium sp.	0	0	3	0	0	0
Allium ursinum	1	0	0	0	0	0
Alnus incana	0	0	0	0	1	0
Alopecurus myosuroides	0	0	9	0	0	0
Althea officinalis	0	0	0	1	0	0
Alyssum alyssoides	0	0	0	2	0	0
Amaranthus hybridus	0	0	1	0	0	0
Ambrosia artemisiifolia	0	0	0	4	0	0
Anacamptis pyramidalis	0	0	12	0	0	0
Anagallis arvensis	0	0	7	0	0	0
Anagallis tenella	0	0	0	0	0	2
Andropogon ischaemum	0	0	1	0	0	0
Andryala integrifolia	0	0	0	1	0	0
Anemone nemorosa	8	0	0	0	0	0
Angelica archangelica ssp. archangelica	0	0	0	0	1	0
Antennaria dioica	0	0	0	0	4	0
Anthemis arvensis	0	0	0	1	0	0
Anthemis cotula	0	0	2	0	0	0
Anthemis ruthenica	0	0	0	3	0	0
Anthriscus caucalis	0	0	2	0	0	0
Anthriscus cerefolium	0	0	0	3	0	0
Apera spica-venti	0	0	0	2	0	0
Aphanes arvensis	0	0	0	0	0	1
Arabidopsis thaliana	0	0	0	3	0	0
Arabis hirsuta	0	0	0	6	0	0
Arabis recta	0	0	0	1	0	0
Arenaria serpyllifolia	0	0	0	23	0	0
Artemisia campestris	0	0	0	3	0	0
Artemisia santonicum	0	0	0	1	0	0
Arum italicum	0	0	4	0	0	0
Asclepias syriaca	0	0	0	3	0	0
Aster tripolium	0	0	0	2	0	0
Astragalus asper	0	0	0	1	0	0
Astragalus cicer	0	0	0	2	0	0
Astragalus onobrychis	0	0	0	1	0	0
Athyrium filix-femina	3	0	0	0	0	0
Atriplex prostrata	0	0	0	1	0	0
Avena fatua	0	0	15	0	0	0
Avena sativa	0	0	4	0	0	0
Avenula pratensis	0	0	0	0	3	0
Avenula pubescens	0	0	0	0	3	0
Ballota nigra	0	0	0	7	0	0
Barbarea vulgaris	0	0	0	0	1	0
Barkhausia taraxacifolia	0	0	1	0	0	0

Berberis vulgaris	0	0	0	1	0	0
Betula nana	0	0	0	0	1	0
Betula pubescens	0	0	0	0	34	0
Betula sp.	3	0	0	0	0	0
Blackstonia perfoliata	0	0	10	0	0	0
Botrychium lunaria	0	0	0	0	1	0
Briza minor	0	0	2	0	0	0
Bromus arvensis	0	0	0	0	0	1
Bromus commutatus	0	0	0	0	0	4
Bromus inermis	0	0	0	3	0	0
Bromus tectorum	0	0	0	8	0	0
Bromus willdenowii	0	0	1	0	0	0
Bryonia alba	0	0	0	1	0	0
Bryonia dioica	0	0	1	0	0	0
Buglossoides arvensis	0	0	0	14	0	0
Bupleurum affine	0	0	0	1	0	0
Cachrys laevigata	0	0	3	0	0	0
Calamagrostis canescens	0	0	0	1	0	0
Calamagrostis epigejos	0	0	0	3	0	0
Calamagrostis purpurea ssp. phragmitoides	0	0	0	0	6	0
Calamagrostis stricta	0	0	0	0	1	0
Camelina microcarpa	0	0	0	4	0	0
Campanula rapunculus	2	0	0	0	0	0
Campanula sibirica	0	0	0	1	0	0
Campanula trachelium	2	0	0	0	0	0
Cardamine amara	0	0	0	0	1	0
Cardaria draba	0	0	0	12	0	0
Carduus acanthoides	0	0	0	1	0	0
Carex atrofusca	0	0	0	0	1	0
Carex bigelowii	0	0	0	0	1	0
Carex canescens	0	0	0	0	9	0
Carex capillaris	0	0	0	0	3	0
Carex distans	0	0	0	11	0	0
Carex elata	0	0	0	3	0	0
Carex hostiana	0	0	0	0	0	1
Carex leporina	3	0	0	0	0	0
Carex montana	9	0	0	0	0	0
Carex muricata aggr.	1	0	0	0	0	0
Carex norvegica	0	0	0	0	1	0
Carex ornithopoda	1	0	0	0	0	0
Carex riparia	0	0	0	0	0	1
Carex rostrata	0	0	0	0	1	0
Carex serotina	0	0	0	0	3	0
Carex sp.1	0	0	0	0	0	3
Carex sp.2	0	0	0	0	0	2
Carex sp.3	0	0	0	0	0	1
Carex spicata	0	0	4	0	0	0
Carex stenophylla	0	0	0	8	0	0
Carex sylvatica	12	0	0	0	0	0
Carex vaginata	0	0	0	0	6	0
Carex vulpina	0	0	0	4	0	0

Carlina vulgaris	0	0	0	1	0	0
Centaurea montana	1	0	0	0	0	0
Centaurea nigra	0	0	0	0	0	6
Centaurea spinulosa	0	0	0	6	0	0
Centaurium pulchellum	0	0	1	0	0	0
Cerastium arvense	0	0	0	0	0	5
Cerastium dubium	0	0	0	1	0	0
Cerastium glomeratum	0	0	3	0	0	0
Cerastium holosteoides	0	0	0	0	0	29
Cerastium semidecandrum	0	0	0	28	0	0
Cervaria rivini	0	0	1	0	0	0
Chaenorhinum minus	0	0	0	0	0	1
Chaerophyllum hirsutum	7	0	0	0	0	0
Chamerion angustifolium	0	0	0	0	0	1
Chamomilla suaveolens	0	0	0	0	3	0
Chenopodium hybridum	0	0	0	2	0	0
Chenopodium polyspermum	0	1	0	0	0	0
Chondrilla juncea	0	0	0	4	0	0
Chrysopogon gryllus	0	0	0	7	0	0
Chrysosplenium alternifolium	0	0	0	0	1	0
Cicerbita alpina	0	0	0	0	1	0
Cichorium intybus	0	0	0	8	0	0
Cirsium brachycephalum	0	0	0	7	0	0
Cirsium canum	0	0	0	5	0	0
Cirsium dissectum	0	0	0	0	0	6
Cirsium eriophorum	0	0	0	0	0	2
Cirsium helenioides	0	0	0	0	4	0
Cirsium sp.	0	0	1	0	0	0
Cleistogenes serotina	0	0	0	1	0	0
Coeloglossum viride	0	0	0	0	1	0
Conopodium majus	0	0	0	0	0	4
Consolida orientalis	0	0	0	1	0	0
Consolida regalis	0	0	0	2	0	0
Cornus sanguinea	0	0	5	0	0	0
Coronilla varia	0	0	0	8	0	0
Crepis foetida	0	0	1	0	0	0
Crepis paludosa	0	0	0	0	2	0
Crepis rhoeadifolia	0	0	0	5	0	0
Crocus sp.	1	0	0	0	0	0
Cruciata pedemontana	0	0	0	2	0	0
Cymbalaria muralis	0	0	0	0	0	1
Cynosurus cristatus	0	0	0	1	0	0
Cytisus scoparius	0	0	1	0	0	0
Dactylorhiza fuchsii	0	0	0	0	0	3
Dactylorhiza maculata	3	0	0	0	0	0
Dactylorhiza sp.	0	0	0	0	0	1
Danthonia decumbens	0	0	0	0	0	1

Descurainia sophia	0	0	0	12	0	0
Dianthus armeria	0	0	1	0	0	0
Dianthus pontederae	0	0	0	7	0	0
Digitalis purpurea	0	0	0	0	0	1
Dipsacus fullonum	0	0	9	0	0	0
Dipsacus laciniatus	0	0	2	0	0	0
Draba nemorosa	0	0	0	2	0	0
Dryopteris filix-mas	3	0	0	0	0	0
Echinochloa crus-galli	0	1	0	0	0	0
Echium vulgare	0	0	0	1	0	0
Elaeagnus angustifolia	0	0	0	1	0	0
Eleocharis acicularis	0	0	0	0	1	0
Eleocharis palustris	0	0	0	11	0	0
Elytrigia repens	0	0	4	0	0	0
Empetrum nigrum	0	0	0	0	7	0
Endymion non-scriptum	0	0	0	0	0	2
Epilobium angustifolium	0	0	0	0	11	0
Epilobium ciliatum	0	0	0	0	3	0
Epilobium lactiflorum	0	0	0	0	1	0
Epilobium montanum	0	0	0	0	0	5
Equisetum fluviatile	0	0	0	0	0	1
Equisetum pratense	0	0	0	0	13	0
Equisetum ramosissimum	0	0	0	3	0	0
Equisetum variegatum	0	0	0	0	3	0
Erica cinerea	0	0	0	0	0	1
Erica tetralix	0	0	0	0	0	3
Erica vagans	0	0	1	0	0	0
Eriophorum angustifolium	0	0	0	0	0	1
Eriophorum vaginatum	0	0	0	0	0	3
Erodium cicutarium	0	0	0	6	0	0
Erysimum diffusum	0	0	0	6	0	0
Erysimum orientale	0	0	0	1	0	0
Erythrea centaurium	0	0	1	0	0	0
Euphorbia amygdaloides	0	0	2	0	0	0
Euphorbia cyparissias	0	0	0	9	0	0
Euphorbia helioscopia	0	0	1	0	0	0
Euphorbia hyberna	0	0	1	0	0	0
Euphorbia palustris	0	0	0	5	0	0
Euphorbia platyphyllos	0	0	1	0	0	0
Euphorbia stricta	0	0	0	0	12	0
Euphorbia virgata	0	0	0	1	0	0
Euphrasia minima	2	0	0	0	0	0
Euphrasia nemorosa	0	0	0	0	0	4
Euphrasia officinalis	0	0	0	0	0	1
Fagus sylvatica	2	0	0	0	0	0
Falcaria vulgaris	0	0	0	6	0	0
Fallopia convolvulus	0	0	0	4	0	0
Festuca pseudovaginata	0	0	0	4	0	0
Festuca pseudovina	0	0	0	36	0	0
Festuca rupicola	0	0	0	1	0	0

Festuca tenuifolia	0	0	0	0	0	3
Festuca vaginata	0	0	0	1	0	0
Filipendula vulgaris	0	0	0	3	0	0
Foeniculum vulgare	0	0	2	0	0	0
Frangula alnus	0	0	0	3	0	0
Fraxinus angustifolia	0	0	6	0	0	0
Galactites elegans	0	0	2	0	0	0
Galeopsis speciosa	0	0	0	0	1	0
Galeopsis tetrahit	0	0	0	0	9	0
Galium boreale	0	0	0	0	5	0
Galium glaucum	0	0	2	0	0	0
Galium lucidum	1	0	0	0	0	0
Galium odoratum	1	0	0	0	0	0
Galium pumilum	2	0	0	0	0	0
Galium saxatile	0	0	0	0	0	16
Galium tricornutum	0	0	1	0	0	0
Galium uliginosum	0	0	0	0	18	0
Gaudinia fragilis	0	0	2	0	0	0
Geranium molle	1	0	0	0	0	0
Geranium pratense	0	0	0	0	0	1
Geranium pusillum	0	0	0	7	0	0
Geranium robertianum	0	0	0	0	0	1
Geum urbanum	4	0	0	0	0	0
Gladiolus illyricus	0	0	1	0	0	0
Gratiola officinalis	0	0	0	2	0	0
Gymnadenia conopsea	0	0	0	1	0	0
Gymnocarpium dryopteris	0	0	0	0	6	0
Gypsophila paniculata	0	0	0	3	0	0
Hedera helix	3	0	0	0	0	0
Helichrysum stoechas	0	0	1	0	0	0
Helictotrichon pubescens	16	0	0	0	0	0
Hieracium piloselloides	1	0	0	0	0	0
Hieracium umbellatum	2	0	0	0	0	0
Hieracium vulgatum	0	0	0	0	2	0
Holosteum umbellatum	0	0	0	13	0	0
Hordeum murinum	0	0	0	5	0	0
Hordeum vulgare	0	0	3	0	0	0
Huperzia selago	0	0	0	0	1	0
Hyoscyamus niger	0	0	0	1	0	0
Hypericum elodes	0	0	0	0	0	1
Hypericum humifusum	0	0	1	0	0	0
Hypericum montanum	1	0	0	0	0	0
Hypericum perfoliatum	0	0	0	1	0	0
Hypericum tetrapterum	0	0	0	0	0	1
Hypochoeris glabra	0	0	0	0	0	1
Hypochoeris maculata	0	0	0	1	0	0
Inula britannica	0	0	0	3	0	0
Inula salicina	0	0	0	3	0	0
Iris pseudacorus	0	0	0	3	0	0
Iris sibirica	0	0	0	2	0	0
Juncus acutus	0	0	0	0	0	9

Juncus compressus	0	0	0	11	0	0
Juncus conglomeratus	0	0	2	0	0	0
Juncus filiformis	0	0	0	0	9	0
Juncus gerardii	0	0	0	8	0	0
Juncus squarrosus	0	0	0	0	0	4
Kickxia spuria	0	0	1	0	0	0
Koeleria cristata	0	0	0	9	0	0
Koeleria javorkae	0	0	0	1	0	0
Lactuca serriola	0	0	3	0	0	0
Lamiastrum galeobdolon	2	0	0	0	0	0
Lamium album	0	1	0	0	0	0
Lamium amplexicaule	0	0	0	2	0	0
Lappula heteracantha	0	0	0	1	0	0
Lapsana communis	0	0	6	0	0	0
Lathyrus montanus	0	0	0	0	0	1
Lathyrus nissolia	0	0	4	0	0	0
Lathyrus palustris	0	0	0	1	0	0
Leontodon taraxacoides	0	0	0	0	0	1
Lepidium campestre	0	0	0	1	0	0
Lepidium crassifolium	0	0	0	2	0	0
Lepidium perfoliatum	0	0	0	1	0	0
Limonium gmelinii	0	0	0	3	0	0
Linaria vulgaris	0	0	1	0	0	0
Linnaea borealis	0	0	0	0	4	0
Linum austriacum	0	0	0	3	0	0
Linum bienne	0	0	17	0	0	0
Linum usitatissimum	0	0	1	0	0	0
Listera ovata	1	0	0	0	0	0
Lonicera caerulea	0	0	0	0	2	0
Lotus pedunculatus	0	0	0	0	0	2
Lotus tenuis	0	0	0	10	0	0
Luzula pilosa	0	0	0	0	5	0
Luzula sp.	0	0	0	0	0	17
Luzula sudetica	0	0	0	0	10	0
Luzula sylvatica	5	0	0	0	0	0
Lycium barbatum	0	0	0	1	0	0
Lysimachia vulgaris	0	0	0	11	0	0
Lythrum virgatum	0	0	0	1	0	0
Malcolmia africana	0	0	0	2	0	0
Malva sp.	0	0	3	0	0	0
Malva sylvestris	0	0	1	0	0	0
Marrubium peregrinum	0	0	0	2	0	0
Matricaria recutita	0	0	1	0	0	0
Medicago arabica	0	0	3	0	0	0
Medicago falcata	0	0	0	8	0	0
Medicago minima	0	0	0	8	0	0
Medicago polymorpha	0	0	9	0	0	0
Melampyrum sylvaticum	0	0	0	0	7	0
Melica nutans	0	0	0	0	2	0
Melilotus altissimus	0	0	1	0	0	0
Melilotus officinalis	0	0	0	2	0	0
Mentha suaveolens	0	0	2	0	0	0

Milium effusum	0	0	0	0	1	0
Minuartia sp.	0	0	0	1	0	0
Molinia arundinacea	2	0	0	0	0	0
Muscari neglectum	0	0	0	1	0	0
Muscari racemosum	0	0	0	3	0	0
Myosotis scorpioides	3	0	0	0	0	0
Myosotis stricta	0	0	0	4	0	0
Myosotis sylvatica	15	0	0	0	0	0
Narcissus pseudonarcissus	1	0	0	0	0	0
Narthecium ossifragum	0	0	0	0	0	2
Odontites rubra	0	0	0	1	0	0
Oenanthe silaifolia	0	0	0	3	0	0
Omalotheca norvegica	0	0	0	0	6	0
Omalotheca sylvatica	0	0	0	0	5	0
Onobrychis viciifolia	0	0	2	0	0	0
Ononis reclinata	0	0	6	0	0	0
Ononis repens	1	0	0	0	0	0
Onopordom acanthium	0	0	0	6	0	0
Ophioglossum vulgatum	1	0	0	0	0	0
Ophrys arachnitiformis	0	0	1	0	0	0
Ophrys scolopax	0	0	2	0	0	0
Ophrys sphegodes	0	0	1	0	0	0
Orchis coriophora	0	0	0	2	0	0
Orchis morio	1	0	0	0	0	0
Orchis palustris	0	0	0	3	0	0
Ornithogalum umbellatum	0	0	0	6	0	0
Orobanche gracilis	0	0	3	0	0	0
Panicum dichotomiflorum	0	0	1	0	0	0
Parnassia palustris	0	0	0	0	3	0
Pastinaca sativa	0	0	0	1	0	0
Petrorhagia prolifera	0	0	0	1	0	0
Phalaris paradoxa	0	0	1	0	0	0
Phleum alpinum	0	0	0	0	23	0
Phleum phleoides	0	0	0	2	0	0
Phleum sp.	0	2	0	0	0	0
Phragmites australis	0	0	0	32	0	0
Phyteuma spicatum L.	2	0	0	0	0	0
Picris rhoeadifolium	0	0	0	1	0	0
Pilosella officinarum	0	0	0	0	0	4
Pinguicula vulgaris	0	0	0	0	2	0
Pinus nigra	0	0	1	0	0	0
Pinus sylvestris	0	0	0	0	5	0
Plantago altissima	0	0	0	2	0	0
Plantago arenaria	0	0	0	1	0	0
Poa alpina	0	0	0	0	3	0
Poa bulbosa	0	0	0	4	0	0
Poa chaixii	3	0	0	0	0	0
Poa humilis	0	0	0	6	0	0
Poa nemoralis	0	0	0	0	3	0
Poa palustris	0	0	0	1	0	0

Polygala sp.	1	0	0	0	0	0
Polygala vulgaris ssp. oxyptera	1	0	0	0	0	0
Polygonatum odoratum	1	0	0	0	0	0
Polygonatum verticillatum	0	0	0	0	2	0
Polygonum amphibium	0	1	0	0	0	0
Polygonum bistorta L.	8	0	0	0	0	0
Polygonum lapathifolium	0	2	0	0	0	0
Polygonum viviparum	0	0	0	0	24	0
Populus alba	0	0	0	1	0	0
Populus nigra	0	0	1	0	0	0
Porella platyfolia	0	0	0	0	0	1
Potamogeton polygonifolius	0	0	0	0	0	1
Potentilla argentea	0	0	0	1	0	0
Potentilla crantzii	0	0	0	0	2	0
Potentilla heptaphylla	0	0	0	2	0	0
Potentilla recta	0	0	0	1	0	0
Potentilla thuringiaca	0	0	0	0	1	0
Poterium sanguisorba	0	0	0	0	0	3
Primula acaulis	8	0	0	0	0	0
Primula vulgaris	0	0	1	0	0	0
Prunella laciniata	0	0	1	0	0	0
Prunus avium	0	0	1	0	0	0
Prunus cerasus	2	0	0	0	0	0
Prunus domestica	0	0	2	0	0	0
Prunus mahaleb	0	0	1	0	0	0
Prunus sp.	1	0	0	0	0	0
Pseudolysima longifolium	0	0	0	1	0	0
Puccinellia distans	0	0	0	1	0	0
Puccinellia limosa	0	0	0	1	0	0
Pyrola minor	0	0	0	0	2	0
Quercus humilis	0	0	10	0	0	0
Quercus petraea	0	0	2	0	0	0
Quercus pyrenaica	0	0	1	0	0	0
Ranunculus arvensis	0	0	1	0	0	0
Ranunculus auricomus	0	0	0	0	10	0
Ranunculus flammula	0	0	0	0	0	2
Ranunculus nemorosus aggr.	2	0	0	0	0	0
Ranunculus pedatus	0	0	0	2	0	0
Ranunculus polyanthemos	0	0	0	2	0	0
Rapistrum rugosum	0	0	2	0	0	0
Rhinanthus alectorolophus	10	0	0	0	0	0
Ribes aureum	0	0	0	1	0	0
Robinia pseudacacia	0	0	0	3	0	0
Robinia pseudoacacia	0	0	1	0	0	0
Rorippa amphibia	0	0	0	1	0	0

Rorippa palustris	0	1	0	0	0	0
Rorippa sylvestris	0	0	0	1	0	0
Rosa foetida	0	0	1	0	0	0
Rosa rubiginosa	0	0	1	0	0	0
Rubus idaeus	0	0	0	0	4	0
Rubus saxatilis	0	0	0	0	4	0
Rubus sp.	7	0	0	0	0	0
Rumex longifolius	0	0	0	0	22	0
Rumex palustris	0	0	0	0	0	1
Rumex stenophyllus	0	0	0	2	0	0
Salicornia prostrata	0	0	0	1	0	0
Salix aurita	0	0	0	0	1	0
Salix cinerea	0	0	0	3	0	0
Salix glauca	0	0	0	0	5	0
Salix lapponum	0	0	0	0	8	0
Salix pentandra	0	0	0	0	1	0
Salix reticulata	0	0	0	0	1	0
Salix starkeana	0	0	0	0	9	0
Salsola kali	0	0	0	1	0	0
Salvia austriaca	0	0	0	1	0	0
Salvia verbenaca	0	0	1	0	0	0
Sambucus ebulus	0	0	1	0	0	0
Saussurea alpina	0	0	0	0	8	0
Saxifraga aizoides	0	0	0	0	2	0
Saxifraga spathularis	0	0	0	0	0	1
Saxifraga stellaris	0	0	0	0	1	0
Saxifraga tridactylites	0	0	0	3	0	0
Scabiosa columbaria	1	0	0	0	0	0
Scabiosa ochroleuca	0	0	0	2	0	0
Schoenoplectus lacustris	0	0	0	7	0	0
Schoenus nigricans	0	0	0	3	0	0
Scirpoides holoschoenus	0	0	0	3	0	0
Scirpus maritimus	0	0	0	11	0	0
Scirpus sp.	0	0	0	0	0	1
Scorzonera cana	0	0	0	11	0	0
Scorzonera hispanica	0	0	0	1	0	0
Scorzonera parviflora	0	0	0	2	0	0
Scutellaria hastifolia	0	0	0	1	0	0
Secale sylvestre	0	0	0	3	0	0
Sedum anglicum	0	0	0	0	0	1
Sedum spurium	1	0	0	0	0	0
Selaginella selaginoides	0	0	0	0	2	0
Senecio aquaticus	0	1	0	0	0	0
Senecio sp.	0	0	3	0	0	0
Senecio vernalis	0	0	0	14	0	0
Serapias vomeracea	0	0	5	0	0	0
Serratula tinctoria	0	0	0	13	0	0
Seseli annuum	0	0	0	1	0	0
Sherardia arvensis	0	0	5	0	0	0
Silene conica	0	0	0	5	0	0
Silene dioica	0	0	0	0	16	0
Silene latifolia	0	0	0	22	0	0
Silene otites	0	0	0	6	0	0

Sisymbrium orientale	0	0	0	3	0	0
Sium latifolium	0	0	0	2	0	0
Solanum dulcamara	0	0	0	1	0	0
Solidago canadensis	0	0	0	1	0	0
Sonchus asper	0	0	23	0	0	0
Sonchus palustris	0	0	0	1	0	0
Spartium junceum	0	0	1	0	0	0
Stachys palustris	0	0	0	3	0	0
Stachys sylvatica	0	0	2	0	0	0
Stellaria alsine	0	0	0	0	0	1
Stellaria longifolia	0	0	0	0	9	0
Stellaria nemorum	0	0	0	0	4	0
Stellaria palustris	0	0	0	0	0	3
Stipa borysthenica	0	0	0	4	0	0
Stipa capillata	0	0	0	3	0	0
Tanacetum vulgare	0	0	0	0	1	0
Tetragonolobus maritimus	0	0	0	15	0	0
Teucrium chamaedrys	0	0	1	0	0	0
Teucrium scorodonia	0	0	0	4	0	0
Thalictrum alpinum	0	0	0	0	4	0
Thalictrum flavum	0	0	0	4	0	0
Thlaspi caerulescens ssp. caerulescens	0	0	0	0	1	0
Thlaspi perfoliatum	0	0	0	1	0	0
Thymus polytrichus	0	0	0	0	0	1
Thymus pulegioides	0	0	1	0	0	0
Thymus serpyllum aggr.	9	0	0	0	0	0
Tilia platyphyllos	1	0	0	0	0	0
Tofieldia pusilla	0	0	0	0	2	0
Torilis arvensis	0	0	4	0	0	0
Tragopogon dubius	0	0	0	3	0	0
Tragopogon orientalis	0	0	0	4	0	0
Trichophorum cespitosum	0	0	0	0	0	1
Trientalis europaea	0	0	0	0	16	0
Trifolium aureum	1	0	0	0	0	0
Trifolium fragiferum	0	0	1	0	0	0
Trifolium incarnatum	0	0	1	0	0	0
Trifolium micranthum	0	0	0	1	0	0
Trifolium montanum	1	0	0	0	0	0
Trifolium ochroleucon	0	0	1	0	0	0
Trigonella monspeliaca	0	0	0	1	0	0
Triticum aestivum	0	0	7	0	0	0
Typha angustifolia	0	0	0	2	0	0
Ulex europaeus	0	0	0	0	0	2
Ulex gallii	0	0	0	0	0	3
Ulmus glabra Huds.	1	0	0	0	0	0
Vaccinium oxycoccos	0	0	0	0	0	1
Vaccinium uliginosum	0	0	0	0	2	0
Valeriana sambucifolia	0	0	0	0	5	0
Valeriana sp.	1	0	0	0	0	0
Valerianella dentata	0	0	5	0	0	0

Valerianella locusta	0	0	0	1	0	0
Veratrum album	0	0	0	3	0	0
Verbascum lychnitis	0	0	0	3	0	0
Verbascum phoeniceum	0	0	0	8	0	0
Verbena officinalis	0	0	19	0	0	0
Veronica beccabunga	0	0	0	0	0	1
Veronica hederifolia	0	0	0	6	0	0
Veronica polita	0	0	0	1	0	0
Veronica prostrata	0	0	0	7	0	0
Veronica triphyllos	0	0	0	1	0	0
Veronica urticifolia	1	0	0	0	0	0
Vicia angustifolia	0	0	0	18	0	0
Vicia bithynica	0	0	6	0	0	0
Vicia hirsuta	0	0	8	0	0	0
Vicia lathyroides	0	0	0	15	0	0
Vicia orobus	0	0	0	0	0	2
Vicia sativa	0	0	39	0	0	0
Vicia tetrasperma	0	0	7	0	0	0
Viola arvensis	0	0	0	2	0	0
Viola biflora	0	0	0	0	11	0
Viola collina	2	0	0	0	0	0
Viola kitaibeliana	0	0	0	6	0	0
Viola reichenbachiana	5	0	0	0	0	0
Viola riviniana	0	0	0	0	0	5
Viola tricolor	0	0	0	0	5	0
Vulpia bromoides	0	0	9	0	0	0
Vulpia myuros	0	0	3	0	0	0
Vulpia sicula	0	0	1	0	0	0

SYNTHESIS OF CHAPTER 1 AND 2

Comparison of Species Diversity in European Arable and Grassland Fields

Gisela Lüscher

1. Introduction

Large areas of productive farmland in Europe are managed as arable or grassland fields. Although both, arable and grassland fields represent land that is consciously shaped by farmers to produce biomass, the two field types differ in the plants that are cultivated, in the manner they are managed and in the duration of vegetation cover. These differences may result in contrasting conditions for wildlife. To account for the peculiarities of the two field types, we conducted separate analyses in Chapter 1 for arable fields and in Chapter 2 for grassland fields. Here, the results of the two chapters were synthesized, aiming to provide an overall comparison of plant, earthworm, spider and bee communities in arable and grassland fields. A comprehensive quantification of the effect of field type would need to take the effect of region into account, which was found to explain most of the general variation in communities (Chapter 1 and 2). However, such a detailed quantification is beyond the scope of this synthesis, which combines data from exclusive arable, exclusive grassland and mixed regions. Instead, data were visually evaluated and discussed on the basis of the results of Chapter 1 and 2 regarding the effects of environmental drivers on the four taxonomic groups.

2. Materials and Methods

2.1. Study Sites and Species Data

Species data from 167 arable fields (Chapter 1) and 357 grassland fields (Chapter 2) were combined to a data set of 524 fields in 109 farms in seven case study regions. Each region provided either exclusively arable fields, exclusively grassland fields or both field types, mostly in the same farms (Table 1).

Table 1: Number of arable and grassland fields and number of farms (in brackets) in the combined data set.

Region	# Arable fields (in # farms)	# Grassland fields (in # farms)	Sum
Marchfeld	56 (16)	-	56 (16)
Stalden	-	65 (19)	65 (19)
Southern Bavaria	49 (16)	32 (15)	81 (16)
Gascony	39 (15)	61 (12)	100 (16)
Homokhátság	23 (14)	88 (18)	111 (18)
Northern Hedmark	-	62 (12)	62 (12)
Wales	-	49 (12)	49 (12)

2.2. Data Analysis

Species richness of arable and grassland fields was compared using sample based accumulation curves due to the unbalanced sampling. Total species richness in each of the two field types was estimated with the first order Jackknife estimator (Palmer 1990). The confidence intervals were generated from 100 permutations of the sampling order. Additionally, for species that occurred exclusively in arable and grassland fields, respectively, accumulation curves were calculated in the same way.

Species composition was compared using nonmetric multidimensional scaling (NMDS) to represent the ordering relationships of fields (Legendre and Legendre 2012). Since the explanatory variable region was identified to predominantly affect species compositions (Chapter 1 and 2), NMDS ordinations were evaluated regarding differences between field types and among regions.

All analyses were performed in R 2.15.3 (R Development Core Team 2012) using package vegan 2.0-6.

3. Results

3.1. Species Accumulation Curves

The analysis of 167 arable and 357 grassland fields (in four and six regions, respectively) revealed that the estimated species richness of all taxonomic groups was lower in arable than in grassland fields (Fig 1). The accumulation curves showed that this is unlikely due to the unbalanced sampling because species richness in any number of samples was lower in arable than in grassland fields. Additionally, fewer species occurred exclusively in arable than in grassland fields.

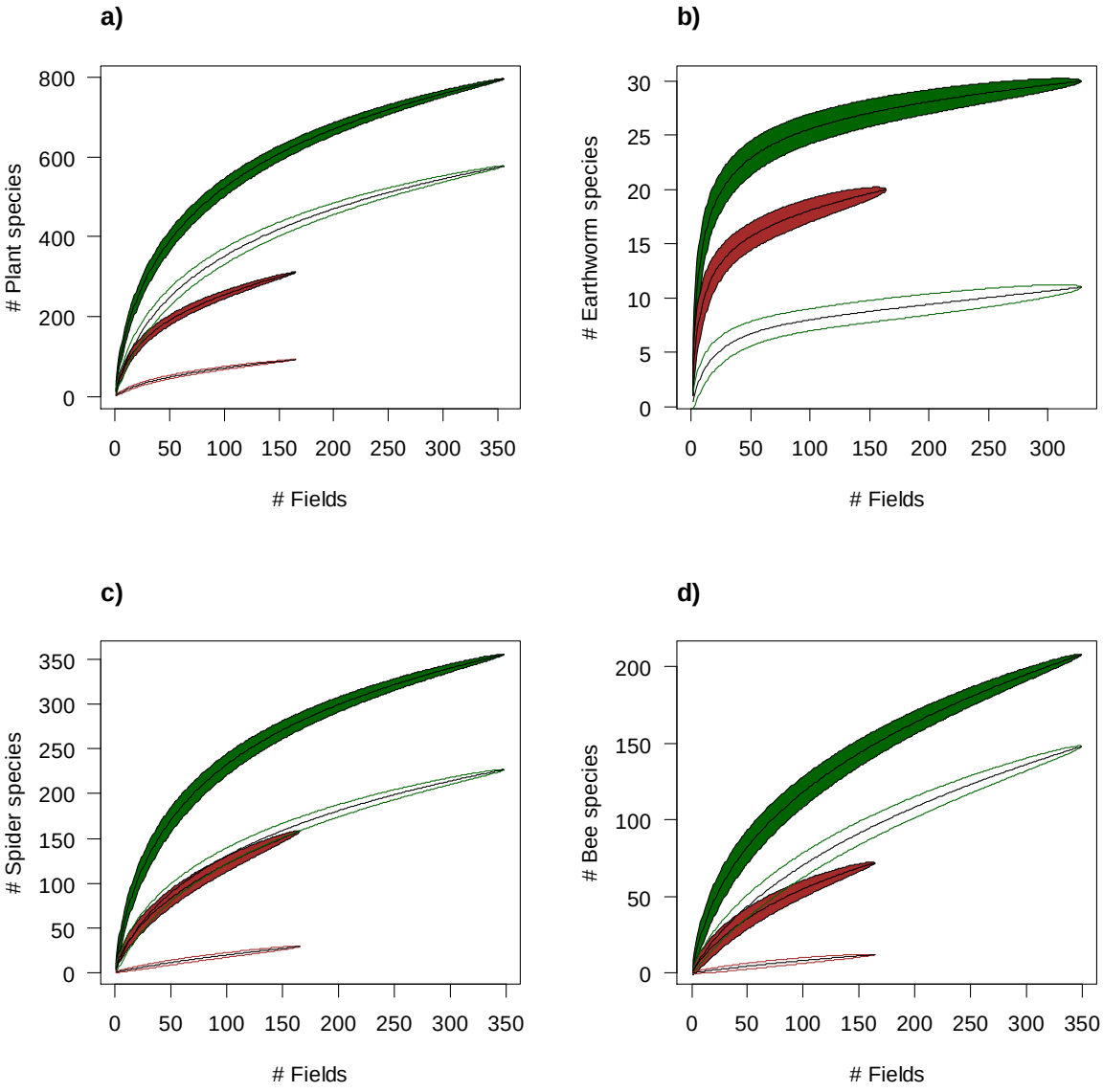

Fig. 1: Total and exclusive species richness estimations (1st order Jackknife) for (a) plants, (b) earthworms, (c) spiders and (d) bees in arable and grassland fields. Polygons indicate 95% confidence intervals. Filled polygons indicate the total species richness: brown colour for arable fields, darkgreen colour for grassland fields. Empty polygons indicate the number of exclusive species: brown line colour for arable fields, darkgreen line colour for grassland fields. For exclusive earthworm species in arable fields no curve was drawn, because only one earthworm species was exclusively found in arable fields.

3.2. Nonmetric Multidimensional Scaling (NMDS) of Species Composition

NMDS displayed distances between fields based on species composition (Fig. 2). Fields that were located close to each other harboured similar abundances of the same species. Fields that were located far apart did not share the same species. If fields formed a small cloud, variability in species composition was relatively low, e.g. the plant species composition in

Stalden. Contrastingly, if distances between fields were large, variability in species composition was relatively high, e.g. spider species composition in Homokhátság.

For plant species composition, NMDS showed a clear separation between arable and grassland fields (Fig. 2a). Arable fields were located in the lower left part of the NMDS, grassland fields in the upper right part. Plant species composition in Gascony, Homokhátság and Northern Hedmark was region-specific. Plant species composition of arable fields in Southern Bavaria was partly similar to that in Marchfeld whereas the composition of grassland fields in Southern Bavaria overlapped with that in Stalden. Another part of plant species composition in Stalden was similar to certain fields in Wales. For earthworm species composition, NMDS showed no clear separation between arable and grassland fields (Fig. 2b). This was especially obvious in regions where both field types were investigated, i.e. Southern Bavaria, Gascony and Homokhátság. Mostly, earthworm composition was similar among several regions except for Gascony. For spider species composition, NMDS showed a relatively clear clump of arable fields in the lower central part (Fig. 2c). Grassland fields were located in the outer, upper part, generally. Spider species composition differed clearly among the three exclusive grassland regions, i.e. Stalden, Northern Hedmark and Wales. In the exclusive arable and mixed regions, i.e. Marchfeld, Southern Bavaria, Gascony and Homokhátság, spider species composition often overlapped. For bee species composition, NMDS showed a number of specific fields, which were located in a broad ring around a dense clump of similar fields (Fig. 2d). In the dense clump, no clear separation between arable and grassland fields and among fields of different regions was recognizable.

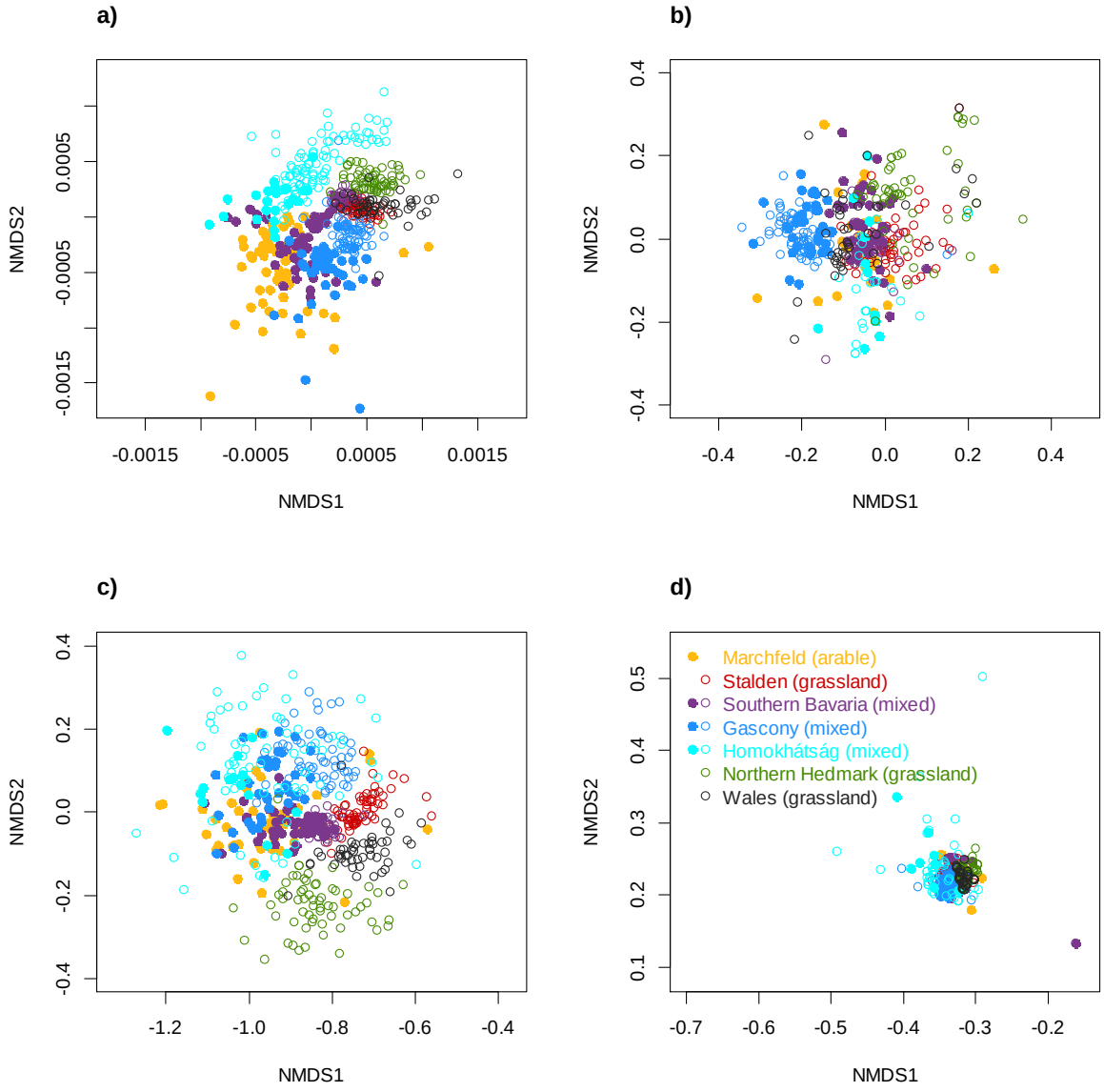

Fig. 2: Nonmetric multidimensional scaling of species composition of log+1-transformed species abundance data of (a) plants, (b) earthworms, (c) spiders and (d) bees, for arable and grassland fields. Filled circles indicate arable fields, empty circles indicate grassland fields. Fields where no species were found had to be excluded from the analysis. Additional fields are not shown due to zooming in the display detail. This concerned 6, 3, 3 and 17 fields for plants, earthworms, spiders and bees, respectively.

4. Discussion

The clear difference of species richness between arable and grassland fields is not surprising as usually the frequent, often severe disturbances and complete removal of vegetation in arable fields provide a more hostile habitat compared to grassland fields. Less species were identified that are able to deal with the conditions of arable fields than with the conditions of

grassland fields. In contrast, differences of species composition between the two field types depended on the taxonomic group. Below, plant, earthworm, spider and bee communities are discussed individually regarding similarities and differences between arable and grassland fields. Results of Chapter 1 and 2 support the interpretation in addition.

4.1. Plants

Weeds in arable fields have different prerequisites compared to plants in grassland. Due to the potential competition for water, light and nutrients between arable weeds and crops, arable weeds are normally strictly controlled (Harker and O'Donovan, 2013). However, arable weeds may benefit crop production in mitigating erosion, promoting arbuscular mycorrhizal fungi or in providing resources for pest predators (Holland, 2004, Hyvönen and Huusela-Veistola, 2008, Brito et al., 2013). In contrast, natural plant communities in grassland provide the basis for forage production. The establishment of plant communities in grassland is driven by the management, and this usually favours fodder plants with high nutritional values (Gaujour et al., 2012). However, a large amount of permanent grasslands are considered as semi-natural habitat across Europe (EEA, 2010). Although plant species richness in grassland is not per se related to a higher biomass production (Adler et al., 2011), a reduction of biomass with the loss of species is a common observation (Hector et al., 1999). Therefore, a rich plant diversity in grassland is favourable. Plant species composition was mentioned by Perner and Malt (2003) as a suitable long-term indicator for changes from arable land to grassland. In our data where grassland fields were at least five years old, plant species composition differed clearly between arable and grassland fields. Despite the differences in the basic life conditions, plant species richness decreased with nitrogen input and increased depending on the diversity of habitats in the surrounding landscape in both field types (Chapter 1, Table 4 and Chapter 2, Table 3). This is presumably due to additional seed sources, because positive effects of the Shannon of habitats around arable fields and the

amount of woody habitats around grassland fields were observed. Overall however, agricultural management more strongly affected plant abundance, species richness and species composition in arable fields than in grassland fields.

4.2. Earthworms

Earthworms are well known to be more abundant in grassland than in arable land (Paoletti, 1999a, van Eekeren et al., 2008, Postma-Blaauw et al., 2010). Although management practices were a main difference between the field types, only nitrogen input affected earthworm abundance in grassland fields (Chapter 2, Table 3). Other effects of agricultural management were not found in our data (Chapter 1, Table 3 and 4). This could be due to several reasons. As Nieminen et al. (2011), Peigne et al. (2009) and Pfiffner and Luka (2007) have shown, soil type, structure, texture and humidity are key factors for the occurrence of earthworms, and these were not considered here. Further, mechanical operations were not distinguished in tillage and other operations. Finally, earthworm communities in both field types were dominated by two species which made up more than 50% of all individuals (*Allolobophora caliginosa* and *A. rosea*). These two species have been found to be quite insensitive to agricultural management (Paoletti 1999a). Therefore, although in grassland fields many more exclusive earthworm species were found, species composition did not clearly differ between arable and grassland fields due to the dominance of *A. caliginosa* and *A. rosea* in both field types.

4.3. Spiders

For spiders, we found clear differences between arable and grassland fields, similar to Schmidt and Tscharntke (2005) and Batáry et al. (2012). Whereas in arable fields around 1/3 of all spider individuals belonged to four very common species, in grassland fields only 4% of all individuals were common species. The main reason for this difference could be the

vegetation structure which is affected by crop type, weed cover and harvest management. Vegetation structure influences strongly the microclimate conditions which are known to influence spider communities (Gibson et al., 1992, Perner and Malt, 2003). In arable fields, significant effects of agricultural management were found (effect of crop type and organic nitrogen input, see Chapter 1, Table 3 and 4). However, in grassland fields, the management variables could only explain variation in species composition but not in species richness or abundance (Chapter 2, Fig. 2 and Table 3; see also Jeanneret et al., 2003; Báldi et al., 2013). This was also the case in a study of Batáry et al. (2008), where spider species richness decreased with nitrogen input in Hungarian cereal fields but no management effect on spiders was found in grassland fields.

4.4. Bees

Bee communities in arable fields were smaller than in grassland fields and consisted mainly of a subsample of the grassland species. Many studies have highlighted that the crucial factors for wild bees are appropriate nesting sites and sufficient flowering plants as food resource during the season (e.g. Muller et al., 2006, Kremen et al., 2007). Arable fields in this study included both, entomophilic and non-entomophilic crops. Therefore, in many of the investigated arable fields no bees were found and crop type had a significant effect on bee abundance and species richness (Chapter 1, Table 3 and 4). In contrast, in nearly all grassland fields, for at least one sampling period, bees were observed which indicated a more continuous availability of flowering plants (compare Mandelik et al., 2012). In both field types, agricultural management practices that were related to a reduction of flower abundance had negative effects, similar to studies that have reported a decline in bee diversity due to intensification of agricultural management (Chapter 1, Table 3 and 4 and Chapter 2, Table 3; e.g. Le Féon et al., 2010). No significant effects of surrounding landscape on bees were found with the exception of bee species composition in grassland (Chapter 2, Fig. 2). Landscape

characteristics have been shown to affect bee communities in other studies, but general conclusions are difficult to identify. Specific habitat features and their accessibility for different groups of bees would need to be accounted for in an assessment of landscape values for bee communities (see also Steffan-Dewenter and Tscharntke 2001, Steffan-Dewenter et al., 2002, Carré et al., 2009, Carvell et al., 2011).

Overall, arable fields harboured less diverse plant, earthworm, spider and bee communities than grassland fields, although a certain number of species also occurred exclusively in arable fields. This could imply that the variability of species composition could be greater in regions with mixed farming. However, this was not confirmed here by NMDS. Regional preconditions, taxonomic group, as well as management and surrounding landscape variables co-determined species diversity of each field.

CHAPTER 3

Gains to Species Diversity in Organically Farmed Fields are not Propagated at the Farm Level

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Gains to Species Diversity in Organically Farmed Fields are not Propagated at the Farm Level

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Abstract

Organic farming is promoted in order to reduce environmental impacts of agriculture, but surprisingly little is known about its effects at the farm level, the primary unit of decision making. Here we report the effects of organic farming on species diversity at the field, farm and regional levels by sampling plants, earthworms, spiders, and bees in 1470 fields of 205 randomly selected organic and non-organic farms in twelve European and African regions. Species richness is, on average, 10.5% higher in organic than non-organic production fields, with highest gains in intensive arable fields (around +45%). Gains to species richness are partly caused by higher organism abundance and are common in plants and bees but intermittent in earthworms and spiders. Average gains are insignificant +4.6% at farm and +3.1% at regional level, even in intensive arable regions. Additional, targeted measures are therefore needed to fulfill the commitment of organic farming to benefit farmland biodiversity.

1. Introduction

Biodiversity is threatened, both at global and regional scales (Butchart et al., 2010; Sachs et al., 2009). During the past decades, agriculture has been a key driver of the loss of biodiversity through intensification of existing farmland and conversion of natural land into cropland (Balmford et al., 2012; Rudel et al., 2009; Tscharntke et al., 2012a). However, farmland also hosts many species that depend on appropriate agricultural management for their survival (Kleijn et al., 2003; Oppermann et al., 2012). Organic agriculture is intended to be a biodiversity-friendly and sustainable farming system (IFOAM, 2012) and is promoted by

many countries as a way of reducing the environmental impacts of agriculture (Stolze and Lampkin, 2009). Although debated, better food quality (Brandt et al., 2011) and less environmental impact (Gomiero et al., 2011) are persuasive arguments that have encouraged an increasing number of consumers to buy organic products. Organic farming is also considered a key strategy for land sharing, i.e. the promotion of biodiversity and food production on the same area of land (Fischer et al., 2011; Hodgson et al., 2010; Phalan et al,. 2011; Tscharntke et al., 2012a).

Evidence generally suggests that organic farming has beneficial effects on biodiversity, but the magnitude of these effects is highly variable (Bengtsson et al., 2005; Fuller et al., 2005; Gabriel et al., 2006; Gabriel et al., 2010; Gabriel et al., 2013; Gomiero et al., 2011; Hole et al., 2005; Tuck et al., 2014; Winqvist et al., 2011). This is due to two major challenges in quantifying the effects of a farming system on biodiversity. First, biodiversity is prohibitively expensive to capture comprehensively and therefore only inferable using proxies, e.g. species richness of certain 'indicator' taxonomic groups (Paoletti, 1999b; Purvis and Hector, 2000). A meta-analysis indicated that organic farming increases species evenness and that organic farming gains to species richness are mainly effects of the abundance of individuals (Crowder et al., 2012). The second challenge is that, while research investigates biodiversity mostly at the field scale, a farmer considers his entire farm when making management decisions (Kelemen et al., 2013). Farms are highly diverse in their internal organization and spatial layout, even within the same geographical region and production type. Farming effects at the field level do not necessarily translate directly to the farm or landscape level (Bengtsson et al., 2005; Gabriel et al., 2006; Gabriel et al., 2010; Hodgson et al., 2010; Kleijn et al,. 2011). Hence, studies at multiple scales are crucial to understanding the impacts of farming systems on biodiversity (Pelosi et al:, 2010).

In a large study on farmland biodiversity, we aimed to quantify the benefits organic farming has on species diversity at field, farm and regional levels across a range of environments from boreal to tropical. In order to address the challenge of the intangible nature of 'biodiversity' as a whole, we analyzed organism abundance, species richness, and species evenness in four taxonomic groups: plants, earthworms, spiders and bees. The groups were selected to represent different habitat compartments (soil, soil surface, and above-ground structures), trophic levels, mobility, and expected responses to agricultural management (Bengtsson et al., 2005; Fuller et al., 2005; Gabriel et al., 2010; Kleijn et al., 2006; Lüscher et al., 2014; Winqvist et al., 2011). In order to cope with the heterogeneity of agriculture, we sampled species in 205 farms in twelve contrasting regions in Europe and Africa using standardized methods (Fig. 1a; Table 1). The regions were homogeneous with regard to environmental conditions, and from each region, 12 to 20 farms were randomly selected, approximately half of them certified organic. No additional constraints were set on the non-organic farms, which could therefore comply with various other statutory or voluntary standards of environmental care (Herzfeld and Jongeneel, 2012). This provided us with representative samples of present-day organic and non-organic farms of a particular production type in every region, thereby avoiding the problematic, and ultimately impossible, exercise of pairing organic and non-organic farms. The consistent assessment of species diversity across three levels of aggregation identifies decreasing gains to species diversity from field to farm and region and recommends targeted measures for the promotion of farmland biodiversity.

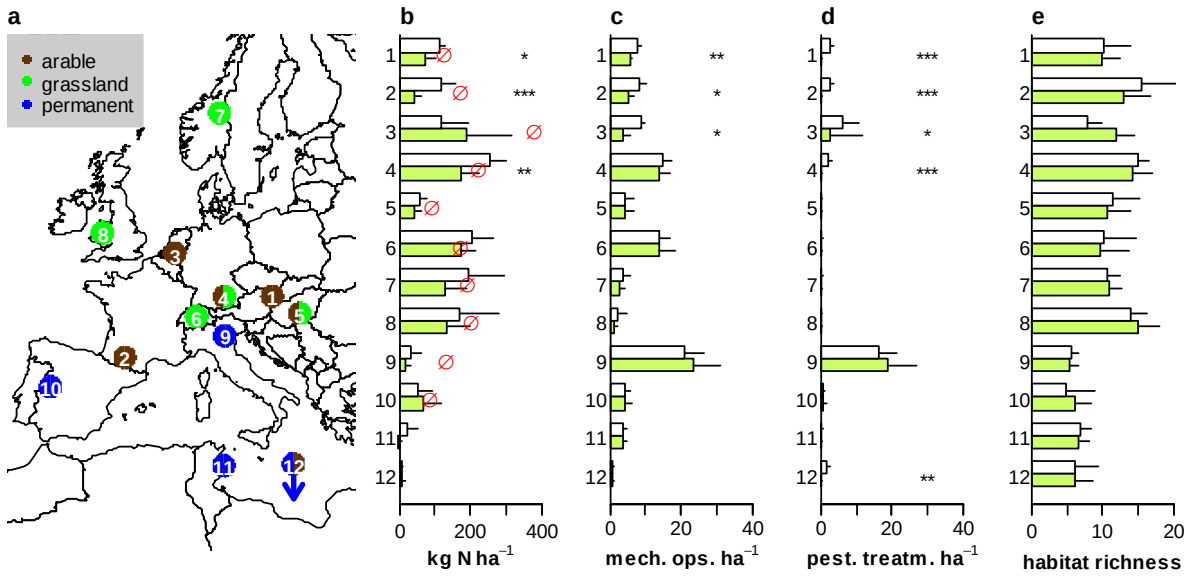

Fig. 1: Management of organic and non-organic farms in twelve regions on two continents. (a) Location of study regions with predominant type of agricultural land use and country boundaries (South, 2011). Regions with bicolor symbol have mixed land use (see Table 1 for details). Region 12 is located in Uganda and not shown on map (b)-(d). Average nitrogen input per hectare (+ standard deviation) (b), average number of mechanical operations (c), average number of pesticide applications (d), and average number of habitats (e) in non-organic (white bars) and organic farms (green bars) in the twelve regions. Red Ø are national average N inputs in 2008 (European Commission, 2011). Significant differences within regions (U-Test) at 0.05, 0.01, and 0.001% are indicated by *, **, and ***, respectively.

Table 1: Locations and environmental characteristics of the study regions.

Nr	Region	Country	Longitude (°)	Latitude (°)	Production type	Altitude (m asl.)	Climate	Rainfall (mm)	MAT* (°C)
1	Marchfeld	Austria	16.7	48.3	Arable crops	140-180	Pannonian	560	9.5
2	Gascony	France	0.5	43.2	Arable crops	197-373	Sub-Mediter.	680	13
3	Gelderland	Netherlands	5.4	51.6	Horticulture	9-35	Atlantic	700	9
4	S. Bavaria	Germany	11.3	48.4	Mixed	350-500	Continental	800	8.5
8	Homokhatsag	Hungary	19.6	46.7	Mixed	93-168	Pannonian	550	10.4
5	Obwalden	Switzerland	8.2	46.9	Grassland	605-1133	Alpine	1300	5.6
6	Hedmark	Norway	11.1	62.4	Grassland	488-886	Boreal	470	0.4
7	Wales	UK	-3.8	52.5	Grassland	450-1085	Atlantic	1500	10
9	Veneto	Italy	11.3	45.4	Vineyards	20-300	Mediterranean	750	12.7
10	Extremadura	Spain	-6.2	40.2	Olives	400-500	Mediterranean	800	16.1
11	Monastir/Madhia	Tunisia	11.0	35.4	Olives	10-100	Semi-Arid	300	22
12	Kayunga	Uganda	32.8	1.0	Mixed	950-1300	Sub-humid	1200	23

* MAT: Mean annual temperature

2. Methods

2.1. Study Regions and Farms

Study regions were selected to reflect major organic farming types in Europe and Africa as well as to be spread across a large gradient of climatic conditions (Table 1). In order to minimize farm selection bias, the regions needed to be as homogeneous as possible with respect to environmental conditions (soil, temperature and precipitation), while still containing a sufficient number of organic and non-organic farms. Basic farm information was obtained from local sources (see Appendix Table S1) and specific exclusion criteria were applied to all farms within each study region, e.g. a minimum portion of area under arable cropping for farms in regions with mixed land use, a minimum farmed area, a particular livestock type, or the cultivation of a particular crop. Hence, sampled farms were representative for a specific combination of region and agricultural types, e.g. vine producers in Veneto, but not for all farms in a region. Organic farms were required to have been certified organic for at least five years prior to the study. No additional constraints were set on the non-organic farms. Out of the eligible farms in each region, 8 to 10 organic and an equal number of non-organic farms were selected at random (see Appendix Table S1). If no agreement was provided by farmers, reserve random selections were used to complete the set.

In the Hedmark region, the total number of farms studied was limited to 12 due to sampling time constraints caused by the short growing season and the complex habitat structure. In the entire Gelderland region, only three non-organic horticultural farms within the study region agreed to participate in the study, in comparison to eleven organic farms. In Homokhátság, only seven organic farms were available for investigation and in Obwalden, a non-organic farmer ceased participation during the study. In Veneto, farms had to be selected from three separate vine areas because there were not enough organic farmers within one single area. In

Wales and Hedmark, organic and non-organic farms were selected in pairs because they were located along a geographical and intensity gradient that made it difficult to get an unbiased subset by random sampling.

Detailed farm data and management information was gathered during structured interviews with farmers. Nitrogen input in kg N ha^{-1} included nitrogen from mineral and organic fertilizers as well as estimated N_2 fixation and was compared to national average nitrogen inputs in kg N ha^{-1} in 2008 (European Commission, 2011). Counts of mechanical operations included e.g. field cultivation, pesticide applications, mowing, turning, bale making and loading. Counts of pesticide applications included natural pesticides. N input, mechanical operations and pesticide applications on fields were totaled and the area-weighted averages per farm were calculated. Gathering of management information in African countries involved more uncertainty than in Europe, especially in multiple cropping systems and the characterization of organic fertilizers.

2.2. Hierarchical Preferential Sampling

The entire area of each study farm was mapped according to the EBONE methodology, a standard habitat mapping procedure for the European scale (Bunce et al., 2008; Bunce et al., 2011). This method is based on a generic system of habitat definitions, General Habitat Categories (GHCs). The habitat qualifiers, which characterize individual habitats with respect to their ecological features, include categories specifically related to farming areas. For our study, the method has been adapted with refined GHC definitions to deal with the specific characteristics of farm holdings. The most important adaptation was the division of the annual crop GHC into four subcategories, namely summer or winter-sown non-entomophilic annuals, entomophilic and/or bee-attracting annuals, and perennials. In addition, the three dominant

plant species were recorded and allowed for comparisons within the regionally most frequent crops.

The first step in mapping was the assessment of the farm area, i.e. all land managed by a farmer. In the second step, the area was mapped to either areal or linear elements. The minimum mappable area for an areal element was 400 m^2, with minimum dimensions of 5 m × 80 m. If the width of an element was smaller than 5 m it was recorded as a linear element with a minimum mappable length of 30 m. Third, based on life form and non-life form categories, a GHC was assigned to every areal and linear element. A farm class (farmed and non-farmed land) and specific environmental and management qualifiers were attributed to all areal elements. The GHCs and qualifiers were chosen from a limited list using specific rules in order to avoid potential multiplicity of codes and mosaics, and to provide a lowest common denominator for linking datasets across study regions. The combination of GHCs and qualifiers allowed a specific separation of habitats with distinct species compositions (e.g. grasslands of different management intensity), while still being general enough for comparison within regions. Across all twelve study regions, the habitat mapping yielded 167 distinct habitats on farmed land, with an average of 26 (range of 13-58) in each region and an average of 7.2 (1-15) per farm (see Appendix Table S2).

Out of all areal or linear elements of a specific farmed habitat on each farm, one plot was randomly selected. On the selected plots, the species of the four taxonomic groups were sampled using standardized protocols (Dennis et al., 2102).

2.3. Species Sampling

Plant species in selected plots of areal habitats were recorded in squares of 10 m × 10 m, well away from the plot edges. In linear habitats, which were by definition less than 5 m wide, plant species were recorded in a rectangular strip of 1 m × 10 m.

Earthworms were extracted at three random locations per plot in all regions except Madhia, where they were completely absent. When soil was humid, 2 liters of a solution of allyl isothiocyanate (AITC), a commercially produced metabolite of glucosinolate, were poured into a metal frame (30 cm × 30 cm) twice at 5 minutes interval (Pelosi et al., 2009) and earthworms appearing at the surface were collected. Thereafter, a soil core of 30 cm × 30 cm × 20 cm deep was excavated, and a single person hand-sorted earthworms from the soil for a duration of 20 minutes.

Spiders were caught with a vacuum shredder (Stihl SH 86-D, Andreas Stihl & Co., Dieburg 64807, Germany) with a tapering gauze bag inserted into the intake nozzle (Schmidt et al., 2005). On each of three sampling dates, five sub-samples were collected for 30 seconds within a sample ring of 0.357 m internal diameter haphazardly pre-placed on the target vegetation within each plot. Sub-samples were immediately transferred to a cool-box. Since a taxonomic catalog of spiders is lacking in the Kayunga region, the region was not sampled for spiders.

Bees were captured with a standard entomological aerial net along a transect of 100 m length and 2 m width during 15 minutes (Banaszak, 1980; Westphal et al., 2008), either identified in the field or immediately transferred into a kill jar. Domesticated bees were counted in the field but not captured. Each plot was surveyed three times during the growing season, but specific timing depended on local conditions.

2.4. Metrics of Species Diversity

Organism abundance and species richness at the field level was calculated by summing all individuals and species per plot, respectively. Species evenness was calculated as

$$E_{\mathrm{var}} = 1 - \frac{2}{\pi}\arctan\left[\sum_{i=1}^{S}\left(a_i - \bar{a}\right)^2 / S\right] \quad (1)$$

where a_i is the log-transformed abundance of species i, ā is the mean of all a_i and S is the total number of species (Crowder et al., 2012; Smith and Wilson, 1996). Data points without or with only one sampled species were omitted from the evaluation of evenness, as no meaningful values could be calculated.

Total species richness at the farm level was calculated by counting all species observed in all sampled habitats on each farm. Abundance at the farm level was calculated by totaling all individuals in all sampled habitats on each farm. Species richness of faunal groups was rarefied individual-based to the smaller value between two and the lowest number of individuals present in all samples of one region using Hurlbert's method (Hurlbert, 1971) implemented in package vegan 2.0-10 in R 3.0.1 (R Development Core Team, 2013). Presented values therefore still reflect differences in the frequency of plots where 0 and 1 individual was sampled.

Total species richness at the regional level was calculated by extrapolating the species-area curves (see Appendix Fig. S1–S4) using the jackknife method of first order (R Development Core Team, 2013). Furthermore, moment-based species accumulation curves together with unconditional standard deviations (Colwell et al., 2004) were calculated for all samples collected on organic and non-organic fields in each region.

2.5. Statistical Analysis

Differences between organic and non-organic within individual regions were tested using Mann–Whitney U Tests. Because interpreting the significances of these tests is not trivial in light of the numerous comparisons (Gelman et al., 2012), we relied on mixed-effects models for assessing the impact of organic farming. In these models, farming effects on each metric of species diversity (S) were calculated for each taxonomic group over all 12 regions. For

organism abundance and species richness, the data were $(S_{ij} \mid \beta, b, x) \sim \text{Poisson}(\mu_{ij})$ from i=1, …, 205 farms in j=1, …, 12 regions. The model is:

$$\log(\mu_{ij}) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + b_{1j} + b_{2ij} \quad (2)$$

$$b_q \sim N(0, \sigma^2), \quad q=1, 2$$

where β_0 is a fixed intercept, β_1 a fixed effect of farming treatment x_{1ij} (organic versus non-organic), β_2 is a fixed effect of the number of sampled habitats per farm x_{2ij}, b_{1j} are random intercepts for country j, and b_{2ij} are random intercepts for farm ij. Random effects b_1 to b_2 are normally distributed with mean 0 and variance σ^2. Random intercepts b_{2ij} accommodate extra-Poisson variance due to over-dispersion (Browne et al., 2005). The significance of term β_1 was calculated by log-likelihood ratio tests with 1 degree of freedom (Zuur et al., 2009, p. 83). For species evenness, mixed-effects model analogous to eq. (2) but with a Gaussian error structure were estimated.

Since the number of sampled habitats on each farm was not equal across farms, it was incorporated into the model for species richness at the farm level as a linear covariate x_{2ij} (Gelman and Hill, 2006, p. 112). The number of samples had no effect on both measurements of species richness at the field level and was omitted from these models.

Maximum likelihood estimation was carried out in R 3.0.1 (R Development Core Team, 2013) using package lme4 (Version 0.999999-2).

The models over all four taxonomic groups are more complex and, hence, offer several possible structures of random effects. For each metric of species diversity, we started therefore with a complex structure of random effects (full model) and subsequently simplified it using sequential log-likelihood ratio tests (Zuur et al., 2009). The most parsimonious model was finally used for inference on the overall organic farming gain to species richness. For each evaluated measure of species richness and abundance (S), the data were species richness

$(S_{kij} \mid \beta, b, x) \sim \text{Poisson}(\mu_{kij})$ of k=1, …, 4 taxonomic groups from i=1,.., 205 farms in j=1,…, 12 regions. The full model is

$$\log(\mu_{kij}) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_{3k} + b_{1j} + b_{2jk} + b_{3ij} + b_{4ijk} + k \cdot b_{5ij} \quad (3)$$

$$b_q \sim N(0, \sigma_q^2), \quad q=1, \ldots, 4$$

$$b_{5ij} \sim N_k(0, \Sigma)$$

where β_0 is a fixed intercept, β_1 is a fixed effect of farming treatment x_{1ij} (organic versus non-organic), β_2 is a fixed effect of the number of sampled habitats x_{2ij} in farm ij, and β_{3k} is a fixed intercept for the taxonomic group k. The term b_{1j} is a random intercept for country j, b_{2jk} is a random intercept for the combination of country j and taxonomic group k, and b_{3ij} is a random intercept for farm ij. The term b_{4ijk} is a random intercept for observations of taxonomic group k in farm ij and accommodates extra-Poisson variance due to over-dispersion (Browne et al., 2005). Random effects b_1 to b_4 are normally distributed with mean 0 and variance σ^2. Term b_{5ij} is a random effect of taxonomic group k within farm ij. In order to account for the nestedness of the observations of the four taxonomic groups within farm ij, b_{5ij} is multivariate normal, with mean 0 and covariance matrix Σ.

The most parsimonious models of both measurements of species richness and organism abundance at field level were full models without the fixed term β_2 and without random terms b_2 and b_3.The most parsimonious models of species richness and organism abundance at farm level was the full model without random terms b_1, b_3 and b_4. Significance of term β_1 was calculated by a log-likelihood ratio test with 1 degree of freedom (Gelman and Hill, 2006).

2.6. Calculation of Organic Farming Gain/Loss

For individual regions and taxonomic groups, organic farming gains (OFGs) and losses were calculated as percent difference of organic farms (OFs) relative to non-organic farms (NOFs)

$$OFG = 100 \cdot \frac{\overline{Y}_{OF}}{\overline{Y}_{NOF}} - 100 \quad , \qquad (4)$$

where $\overline{Y}$ is the mean species richness in organic and non-organic farms in each region.

The standard deviation (Hedges et al., 1999) of the OFG is

$$sd_{OFG} = 100 \cdot \sqrt{\frac{sd_{OF}^2}{n_{OF}\overline{Y}_{OF}^2} + \frac{sd_{NOF}^2}{n_{NOF}\overline{Y}_{NOF}^2}} \quad , \qquad (5)$$

where sd is the standard deviation and n is the number of observations in each group.

Organic farming gains and losses across regions and taxonomic groups were calculated based on coefficients estimated from mixed-effect models (eqs. 2 and 3). At the population mean, the expected effect of organic farming is $e^{\beta 0 + \beta 1} / e^{\beta 0} = e^{\beta 1}$ and hence

$$OFG = 100 \, (e^{\beta 1} - 1) \qquad (6)$$

2.7. Area-weighted Random Resampling

In order to assess the diminishing of organic farming gains to species richness from field to farm, we resampled fields according to their proportion of total farm area. Specifically, we generated 100 random sequences of all sampled habitats per farm weighted by their areal proportion (Venables and Ripley, 2002, p. 111). This resulted in random sequences of habitats predominantly starting with those habitats with high areal proportions. We then calculated the accumulation of species richness along each sequence and, based on the 100 realizations, the mean accumulation of species richness per farm. Finally, we fitted mixed-effects models for each taxonomic group at each number of sampled habitats using eq. (2) and calculated organic farming gains using eq. (6).

3. Results

3.1. Farm Structures and Management

The investigated regions represented various production types with a low to medium intensity of farming, thus accounting for a relatively large portion of global agriculture (Conant et al., 2013). Regional average N input ranged from 5 to 215 kg N ha^{-1} (Fig. 1b), average farm sizes per region were between 3 and 142 ha (see Appendix Table S1). Organic farms were characterized by lower mean nitrogen inputs (-22.4%, $P\chi_1^2$ <0.02; Fig. 1b), fewer mechanical field operations (-9.3%, $P\chi_1^2$ < 0.08; Fig. 1c), and fewer pesticide applications (-75.9%, $P\chi_1^2$ <0.001; Fig. 1d) than in their non-organic counterparts. Organic farms did not, on average, have a higher number of habitat types or a higher areal proportion of semi-natural elements (Fig. 1e).

3.2. Species Richness in Production and Non-production Habitats

Since habitats present in each region differed, a comparison at the field level was only possible for the most frequently observed habitats per study region. Depending on the region, the most frequent habitats managed with the primary aim of agricultural production were winter or summer-sown non-entomophilic crop fields, fertile grasslands, vineyards or olive groves (see Appendix Table S2). The most frequent non-production habitats, e.g. managed for access to land, wind shelter or as part of an agri-environmental scheme, were grassy or shrubby strips along field or water edges.

Organic farming was beneficial to species richness of plants and bees in production fields in many regions, but differences were rarely significant if tested within each region separately (Fig. 2a). Mixed-effects models estimated by maximum likelihood show that in all regions combined, organic farming gains to species richness in production habitats were +17.1% ($P\chi_1^2$

<0.01) for plants, +6.3% (ns) for earthworms, +1.2% (ns) for spiders, +13.6% (ns) for bees. Across all four taxonomic groups and all regions, 10.5% ($P\chi_1^2$ <0.02) more species were found in organic than in non-organic production fields. This significant positive effect of organic farming on species richness arises from the fact that all groups responded positively, although only the difference in plants was significant alone. Differences in species richness between organic and non-organic production fields were highest in winter-sown crops in Marchfeld, Gascony, and Southern Bavaria as well as in horticultural fields in Gelderland (+45.5%, $P\chi_1^2$ <0.001 on average across these four regions and the four taxonomic groups). Effects were similar if the regionally most frequent individual crops (winter wheat or alfalfa) were compared (see Appendix Fig. S5). These crops were not necessarily present on all farms because details of the crop rotation were not a selection criteria but rather a possible difference between farms. The four regions also showed significant differences in management intensity between organic and non-organic farms (as illustrated by N input, the number of mechanical operation per ha and the number of pesticide applications per ha; Fig. 1b-d). Average regional gains to species richness in production habitats were positively correlated to regional average N input per ha (Spearman's $\rho = 0.68$, $P < 0.05$).

In contrast to production habitats, organic farming did not alter species richness in non-production habitats (-3.6% (ns) for plants, +13.4% (ns) for earthworms, -7.1% (ns) for spiders, +9.1% (ns) for bees, and -0.7% (ns) overall; Fig. 2b).

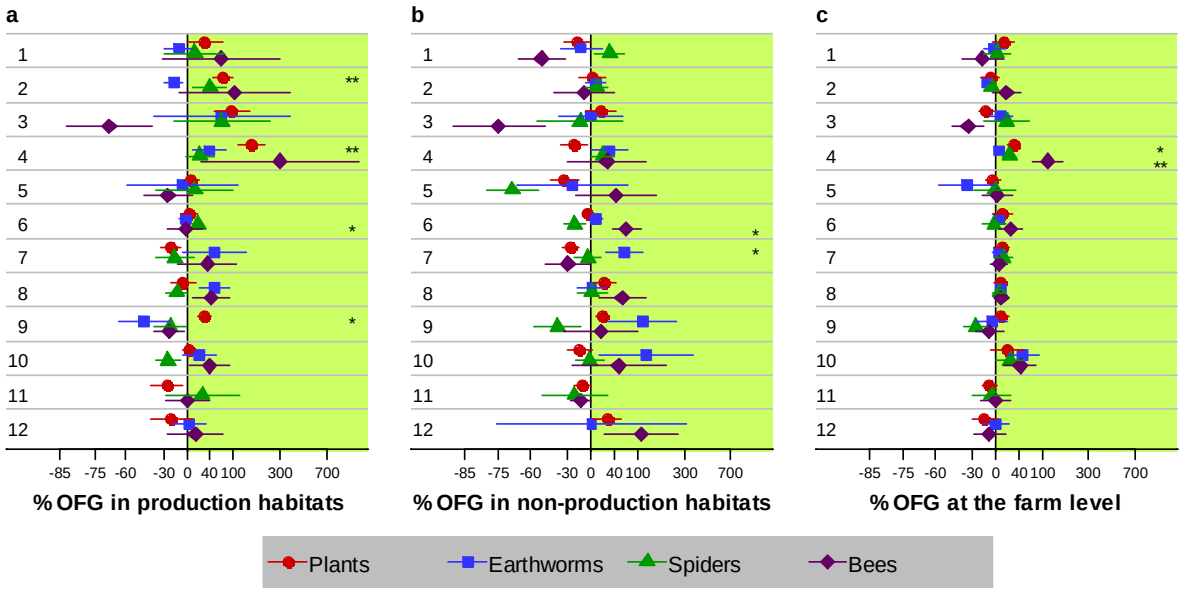

Fig. 2: Organic farming gains and losses (OFG) to species richness in twelve regions. Organic farming gains/losses (± standard deviation) to species richness in the regionally most frequent production habitats (a), in the most frequent non-production habitats (b), and on total species richness per farm (c), for the four taxonomic groups of plants, earthworms, spiders, and bees in the twelve regions shown in Fig. 1a. X-axes are log-scaled to equalize distances on both sides of parity. Significant differences within regions (U-Test) at 0.05, 0.01, and 0.001% are indicated by *, **, and ***, respectively.

3.3. Organic Farming Gains to Species Richness at the Farm Level

As assessed by hierarchical preferential sampling, organic farms tended to have higher total species richness than non-organic farms. Across all regions, organic farming gains were +4.8% (ns) for plants, +3.1% (ns) for earthworms, +3.2% (ns) for spiders, +12.8% ($P\chi_1^2$ <0.05) for bees, and +4.6% ($P\chi_1^2$ <0.1) across all four taxonomic groups. Gains to total species richness were strongest in Bavarian mixed farms, as well as in olive farms in Extremadura, and were consistently positive in the grassland farms in Obwalden, Hedmark, and Wales (Fig. 2c). These results reflect diminished organic farming gains for biodiversity when observed at the farm level as compared to the field level. A weighted random resampling procedure with the areal proportion of different habitats per farm as weights indicated that organic farming gains to species richness decrease if more of the smaller habitats on the farm are included (Fig. 3a-d). The resampling mimicked random species

sampling, in which samples are more likely drawn in habitats with a larger areal proportion, in this case, predominantly production habitats. The fading was especially pronounced where organic farming gains to production habitats were large, namely with plants and bees and in regions with arable cropping (Fig. 3e). Gains to species richness of spiders also tended to decrease with more sampled habitats.

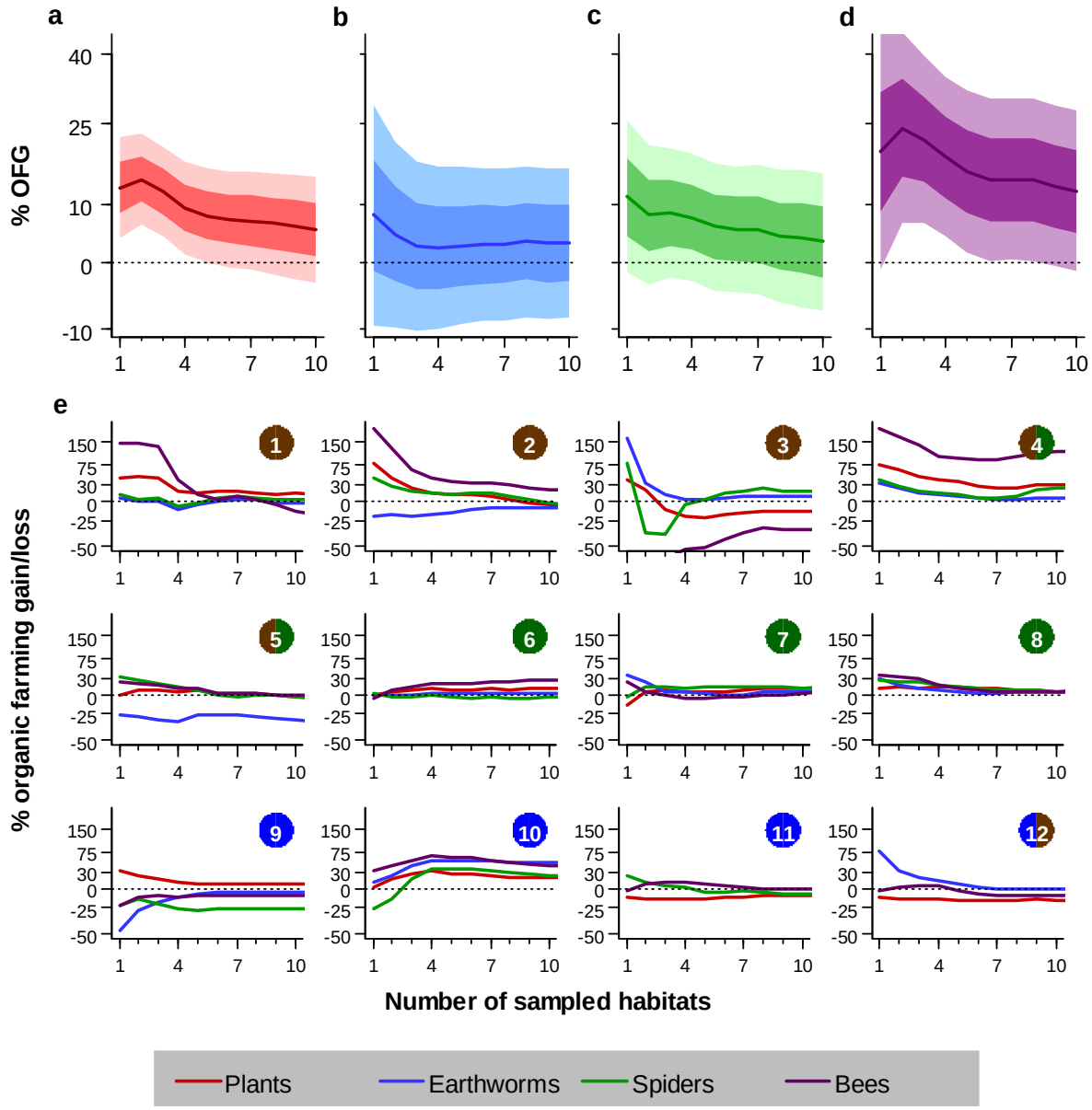

Fig. 3: Organic farming gains and losses to species richness fade from field to farm. (a-d), Species numbers of plants (a), earthworms (b), spiders (c), and bees (d) depending on the number of resampled habitats in the twelve regions shown in Fig. 1a. Lines show average organic farming gains/losses (OFG) estimated from mixed-effects models, shaded areas are approximate 50% and 95% confidence intervals. (e) Species numbers depending on the number of resampled habitats for the twelve individual regions. Y-axes are log-scaled to equalize distances on both sides of parity. Numbers and coloured circles correspond to the twelve regions as displayed in Fig. 1a.

3.4. Effects of Organic Farming on Organism Abundance and Species Evenness

Organic farming gains to organism abundance and to species richness were strongly correlated (Spearman's $\rho = 0.67$, $P < 0.001$, over all four groups in production and non-production habitats and at farm level; see Appendix Table S3). Consequently, trends for organic farming gains were also detected for the cumulated cover abundance of plants (+9.0%, ns) and the number of individuals of earthworms (+3.8, ns), spiders (+5.7%, ns) and bees (+23.8, ns) in production habitats (Fig. 4a). As with species richness, organic farming gains to organism abundance across all four taxonomic groups were highest for the four regions with intensive arable or horticultural fields (+25.6%, $P\chi_1^2 < 0.05$ vs. +8.5%, ns, across all regions). Rarefying faunal species richness to equal numbers of sampled individuals showed that a positive but insignificant gain of organic farming remained (+6.9%, ns, for bees; +2.0% for spiders and +9.8% for bees; see Appendix Fig. S6). Organic farming had no significant effect on species evenness in production habitats, with the exception of plants in the four most intensive regions (+40%, $P\chi_1^2 < 0.01$; see Appendix Fig. S7a).

Organic farming also had no significant effects on abundance or evenness in non-production habitats (Fig. 4b and Appendix Fig. S7b) and at the farm level (Fig. 4c and Appendix Fig. S7c).

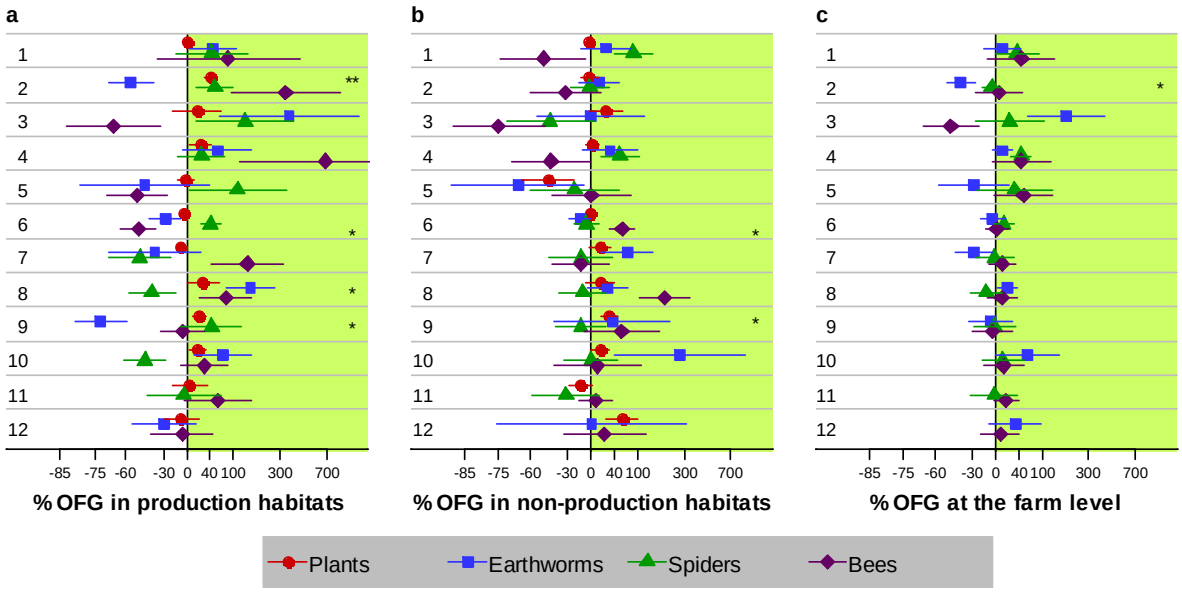

Fig. 4: Organic farming gains and losses to organism abundance in twelve regions. Organic farming gains/losses (± standard deviation) to organism abundance for the four taxonomic groups (cumulated cover for plants and number of individuals for faunal groups) in the regionally most frequent production habitats (a), in the most frequent non-production habitats (b), and on total organism abundance per farm for the faunal groups (c). X-axes are log-scaled to equalize distances on both sides of parity. Numbers on Y-axis indicate the twelve regions shown in Fig. 1a. Significant differences within regions (U-Test) at 0.05, 0.01, and 0.001% are indicated by *, **, and ***, respectively.

3.4. Organic Farming Gains to Species Diversity at Regional Level

There were considerable differences in species richness between regions for the four taxonomic groups. However, in the majority of regions, species accumulation curves from samples in organic and non-organic farms had similar shapes (see Appendix Fig. S1–S4). Extrapolated regional species numbers from these curves differed little between organic and non-organic farms (see Appendix Fig. S8a) and the overall organic farming gain was +3.1% (ns). The organic farming effect on regional organism abundance was +12.4% (ns, see Appendix Fig. S8b) and on regional species evenness -6.3% (ns, see Appendix Fig. S8c).

4. Discussion

The evidence from 205 European and African farms suggests substantial organic farming gains to species richness of plants and bees in production habitats in intensive arable regions, which is in agreement with several other studies conducted at the field level (Bengtsson et al., 2005; Fuller et al., 2005; Gabriel et al., 2006; Gabriel et al., 2010; Gomiero et al., 2011; Hole et al., 2005; Tuck et al., 2014; Winqvist et al., 2011). Organic farming benefits to species richness in production fields increased with regional average nitrogen input, as well as with differences in nitrogen input between organic and non-organic farms. This agrees with a recent meta-analysis (Tuck et al., 2014) as well as with an investigation in wheat fields, which indicated that organic farming gains in biodiversity are proportional to losses in yield (Gabriel et al., 2013). However, organic farm gains to species richness at the field level fade when observed at a greater spatial level, from a significant +10.5% overall taxa at the field level to an insignificant +4.6% at the farm and +3.1% at the regional level. Our finding is in agreement with the few studies that compared organic and non-organic practices at farm or landscape level and found weaker effects at higher levels of aggregation (Hodgson et al., 2010; Gabriel et al., 2010). In contrast to earlier studies, we aimed at a comprehensive assessment of all habitats affected by farming activities, including non-productive habitats, such as unpaved tracks or field margins. This allowed us to account for possible differences in habitat composition between farms, which are of crucial importance for biodiversity at farm level (Aviron et al., 2009; Benton et al., 2003; Billeter et al., 2008; Pelosi et al., 2010).

Species richness at the farm level is a combination of farming effects at the field level and the composition of farmland habitats on each farm. This interaction is exemplified by comparing data from Extremadura and Veneto. In Extremadura, organic and non-organic olive groves did not differ in species richness because in both farming systems, the primary management is

harrowing to control weeds and reduce competition for soil water (Lozano-Garcia and Parras-Alcántara, 2013). Herbicides are primarily used to control weed invasion from margins and reduce species richness in non-organic, non-production strips of grass and shrubs. Consequently, less species are found in non-organic than in organic farms. In contrast, herbicide use in non-organic vineyards in Veneto reduced floral species richness (Nascimbene et al., 2012), whilst the application of natural pesticides and organic weed control may have reduced richness of faunal groups in organic vineyards (Paoletti, 1999a). Similar habitat richness in all farms resulted in higher floral but lower faunal species richness on organic than non-organic Venetian farms.

Habitat composition was taken into account in the resampling procedure, which highlights a continuous decrease in the positive effects of organic farming on plant and bee species richness as more farm habitats are sampled. Such fading from field to farm may be explained by two processes: the regional pool of farmland species may be limited and simply attained faster on organic farms, or additional species in organic production habitats are ubiquitous, invading more easily from boundaries into fields and contribute little to the total species richness per farm. Ubiquity of species appears to be more likely than limited pools since the individual farms contained, on average, only 27% (±6.8% standard deviation) of all plant species and 24% (±13.2%) of all bee species found in the region. We further calculated the occurrence of each plant and bee species relative to all samples in a region as a measure of species rarity, but did not find organic farming effects on species rarity. This suggests that the higher species richness in organic production fields is mostly due to common species, which contribute relatively little to total farm species richness because they are frequently found in other habitats of each farm.

There was a striking correspondence between gains to species richness and organism abundance across all regions and taxonomic groups. While this is not surprising and is a well-known property of species richness (Gotelli and Colwell, 2001; Crowder et al., 2012; Lüscher et al., 2014), it shows that a higher abundance of individuals is likely the most important effect of organic farming on species richness. Hence, organic farming is not significantly increasing the number of species present in a given number of individuals but sustains a higher number of individuals in a given sampling unit.

Investigating species diversity across multiple regions and taxonomic groups using standardized methodology also substantially complements our understanding of the effects of organic farming on biodiversity by showing where there are no significant effects. Most prominently, organic farming contributed little to habitat heterogeneity, which is of key importance for farmland biodiversity (Aviron et al., 2009; Benton et al., 2003; Billeter et al., 2008; Pelosi et al., 2010). Organic and non-organic farms did not differ in average habitat richness and thereby, in their potential to host exclusive species in any of the investigated regions. Organic farming effects on earthworm and spider richness and abundance were highly region-specific but marginal over all regions. Furthermore, we found significant gains to species evenness in plants in arable fields only, in contrast to a recent meta-analysis based on 81 studies (Crowder et al., 2012). This shows that any evaluation of farming effects on biodiversity requires critical consideration of the investigated taxonomic groups and geographical coverage (Tuck et al., 2014; Batáry et al., 2011).

Organic farming gains in the two investigated African regions were surprisingly small and did not differ from European regions. Interestingly, plant species richness in both regions tended to be lower in organic than in non-organic production fields. Due to the costs of organic certification and market access, organic growers may invest more labor in weed control than

some of their non-organic counterparts (Chongtham et al., 2010). In addition, inputs to agriculture are relatively low in both regions and, hence, differences between organic and non-organic management are small (Khedher and Nabli, 2003).

Despite substantial variation between taxonomic groups and regions, the majority of the average effects of organic farming on species diversity demonstrate a positive tendency. This is true for most of the non-significant effects on species richness, abundance and evenness in productive fields and at farm and regional level. Hence, organic farming tends to sustain species diversity to a higher degree than non-organic farming by allowing more individuals to survive in a given unit of agricultural habitat.

We conclude that organic farming represents a step in the right direction toward preserving farmland biodiversity. Yet, the gains fade at the farm level due to the equilibrating effect of non-production habitats, which are similar in both farming systems. Therefore, land sharing by present-day organic farming alone is unlikely to halt the current global decline in farmland biodiversity (Phalan et al., 2011; Sachs et al., 2009). Additional land-sparing measures that maintain and increase habitat diversity and quality, such as directed agri-environment schemes (Gabriel et al., 2006; Kleijn et al., 2003; Kleijn et al., 2011), set-aside areas (Aviron et al., 2009; Kleijn et al,. 2006), and management contracts for habitats of rare species (Oppermann et al., 2012) are urgently needed. Implementation of these measures in organic farming guidelines (IFOAM, 2012; Stolze and Lampkin, 2009) should be intensified in order to boost its performance in terms of promoting farmland biodiversity. Our study highlights that only by means of such targeted measures it is possible to accommodate the dual objectives of food production and biodiversity conservation on farmland.

Acknowledgments

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Additional information

Author Contributions: F.H., P.J., D.B., P.D., W.F., J.K.F., R.H.G.J., M.K., G.M., M.G.P., P.P. and J.P.S. conceived the project; M.A., Y.A., D.B., K.B., A.B., J.P.C., P.D., S.E., W.F., M.D.F., T.F., J.K.F, S.G., I.R.G., T.G., G.G.B., G.L., G.J., R.H.G.J., E.K., M.K., A.K.-H., G.M., C.N., J.O., M.L.O., M.G.P., F.J.P., J.P.S., M.K.S., N.S., D.S., S.W. coordinated field sampling and data processing in the respective study region; M.K.S. and G.L. analysed the data, together with P.J., A.H., L.A.T., S.W. and F.H.; M.K.S. wrote the paper with input from all authors.

Appendix

Table S1: Number and size of sampled farms. Group means (standard deviation) for organic farms (OF) and non-organic farms (NOF) in the study regions as well as source of initial information used for random selection.

Nr	Region	# of farms		Farm area (ha)		Source of initial farm information
		NOF	OF	NOF	OF	
1	Marchfeld	8	8	64.1 (25)	72.7 (37)	Austrian Ministry of Agriculture (INVEKOS)
2	Gascony	8	8	101 (62)	38.7 (30)	Gers & Hte-Garonne Chambers of Agriculture and Dynafor farm database
3	Gelderland	3	11	10.8 (7)	22.1 (12)	Biologica and Ministry of Agriculture, Nature and Food Quality
4	S. Bavaria	8	8	65.2 (29)	54.9 (31)	Bavarian State Research Center for Agriculture
5	Homokhátság	11	7	88.3 (50)	107 (44)	Kiskunság National Park Directorate, Bács-Kiskun County Agricultural Chamber, Biokontroll Hungária Nonprofit Ltd.
6	Obwalden	9	10	9.58 (5.1)	10.1 (3.5)	Office for Agriculture, Canton of Obwalden
7	Hedmark	6	6	13.8 (5.7)	17.5 (9)	Applications for Farm Subsidies database, Norwegian Agricultural Authority.
8	Wales	10	10	152 (112)	132 (83)	Organic Farming Wales database & Farm Business Survey
9	Veneto	9	9	28.8 (34)	18.1 (6.8)	Local producer associations
10	Extremadura	10	10	7.68 (11)	8.28 (5.7)	Organic Farming Committee of Extremadura and cooperative of olive producers of North Extremadura (ACENORCA)
11	Monastir/ Madhia	10	10	17 (18.6)	132 (268)	Ministry of Agriculture, regional department
12	Kayunga	8	8	3.5 (2.9)	2.4 (1.5)	Parish Unit Administrations of Nakseeta and Nsotoka

Table S2: Habitat characteristics per region. Values are means (and standard deviations) of sampled habitats in organic farms (OF) and non-organic farms (NOF) as well as most frequently observed production and non-production habitats per region.

Nr	Region	Mean # of sampled habitats		Most frequent habitats	
		NOF	OF	Production	Non-production
1	Marchfeld	7.6 (2.5)	7.8 (1.67)	Winter-sown crop	Herbaceous strip
2	Gascony	11 (2.88)	9 (3.07)	Winter-sown crop	Grass strip
3	Gelderland	7 (2)	7.5 (1.57)	Horticultural crop	Grass strip
4	S. Bavaria	7.5 (0.926)	8.4 (1.69)	Winter-sown crop	Grass strip
5	Homokhátság	8.2 (2.75)	8.3 (2.63)	Summer-sown crop	Water edge
6	Obwalden	5.4 (2.07)	6 (2.16)	Fertile grassland	Herbaceous strip
7	Hedmark	10 (2.28)	9.7 (1.86)	Fertile grassland	Herbaceous strip
8	Wales	11 (1.51)	11 (2)	Fertile grassland	Water edge
9	Veneto	4.1 (0.782)	4.1 (1.05)	Vineyard	Grass strip
10	Extremadura	3.5 (3.17)	3.9 (1.73)	Olive grove	Line of shrub
11	Monastir/Madhia	6.7 (1.34)	6.6 (1.58)	Olive grove	Grass strip
12	Kayunga	5.6 (2.92)	5.8 (2.55)	Pineapple/Banana	Grass fallow

Table S3: Correlations between organic farming gains to species richness and organism abundance. Shown are Spearman's rank correlation coefficients together with significance levels (* 0.05%, ** 0.01%, and *** 0.001%, ns non-significant). Organism abundance was not quantified for plants at farm level.

Level	Plants	Earthworms	Spiders	Bees
Most-frequent production habitats	0.55^{ns}	0.73*	0.56^{ns}	0.90***
Most-frequent non-production habitats	0.66*	0.77**	0.75**	0.78**
Farm	-	0.71*	0.37^{ns}	0.19^{ns}

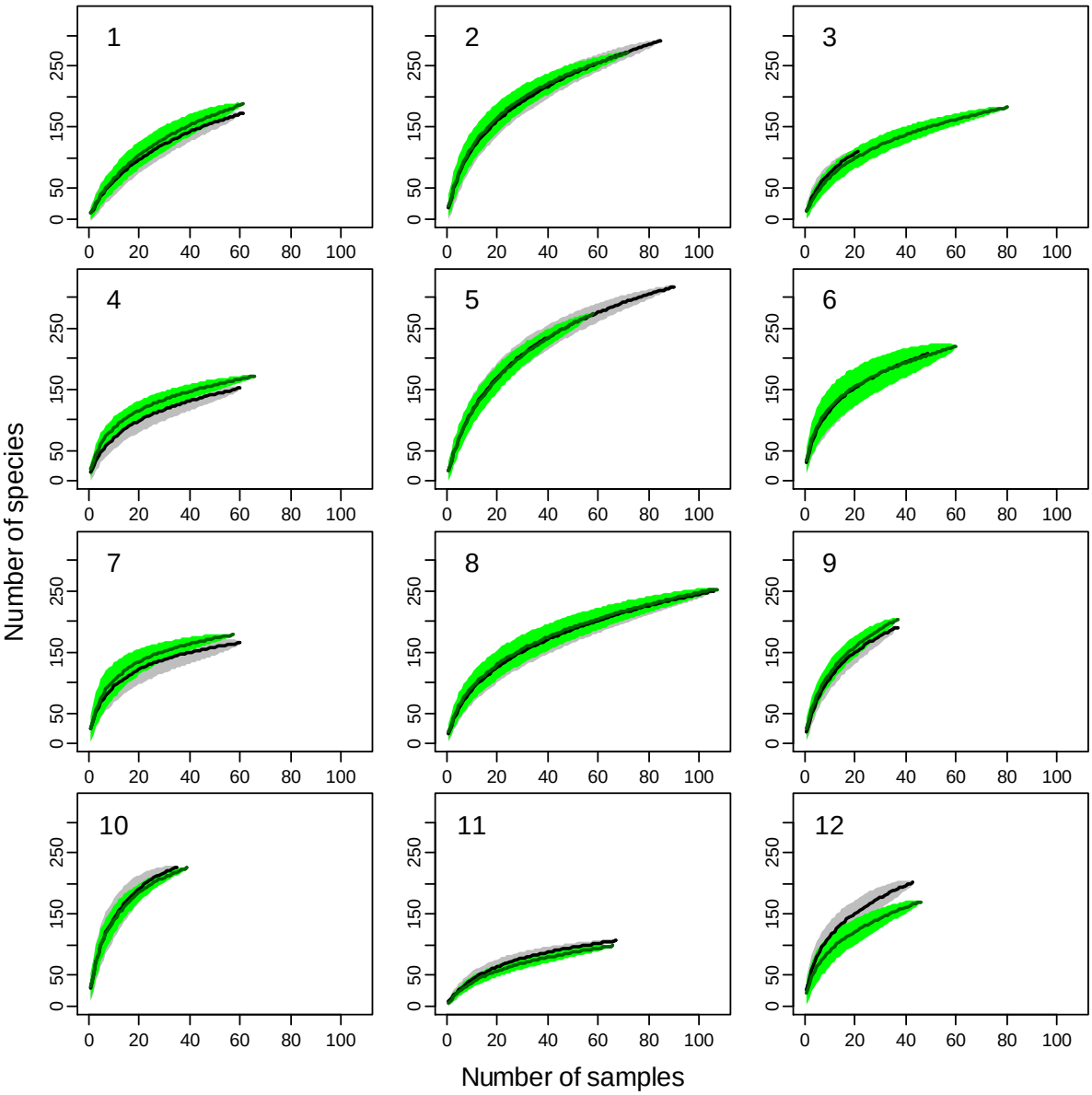

Fig. S1: Plant species accumulation under organic and non-organic farming in twelve regions. Accumulation of the number of plant species with the number of samples in organic (green) and non-organic (grey) fields. Numbers indicate the twelve regions as displayed in Fig. 1a.

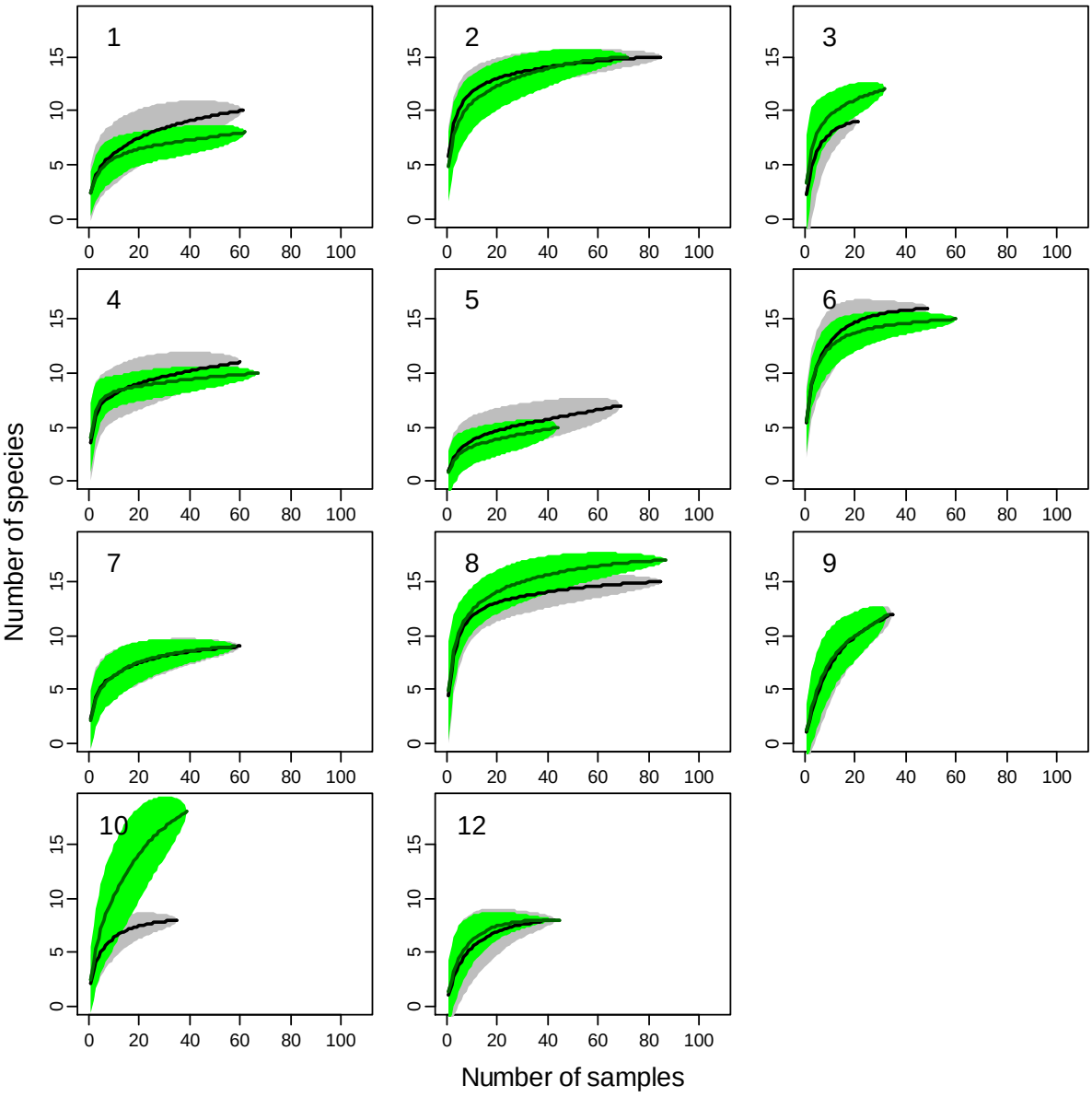

Fig. S2: Earthworm species accumulation under organic and non-organic farming in twelve regions. Accumulation of the number of earthworm species with the number of samples in organic (green) and non-organic (grey) fields. Numbers indicate the twelve regions as displayed in Fig. 1a.

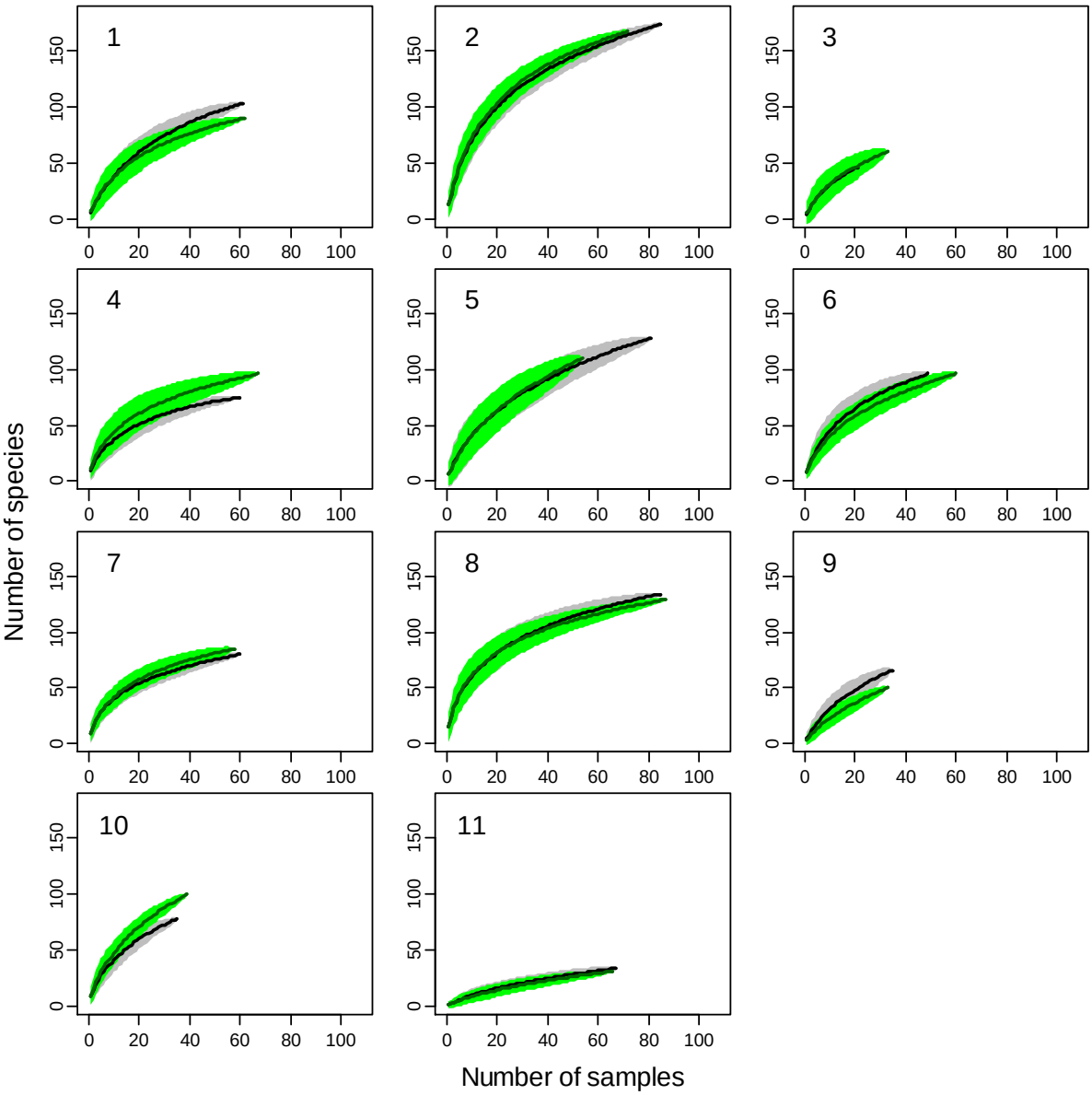

Fig. S3: Spider species accumulation under organic and non-organic farming in twelve regions. Accumulation of the number of spider species with the number of samples in organic (green) and non-organic (grey) fields. Numbers indicate the twelve regions as displayed in Fig. 1a.

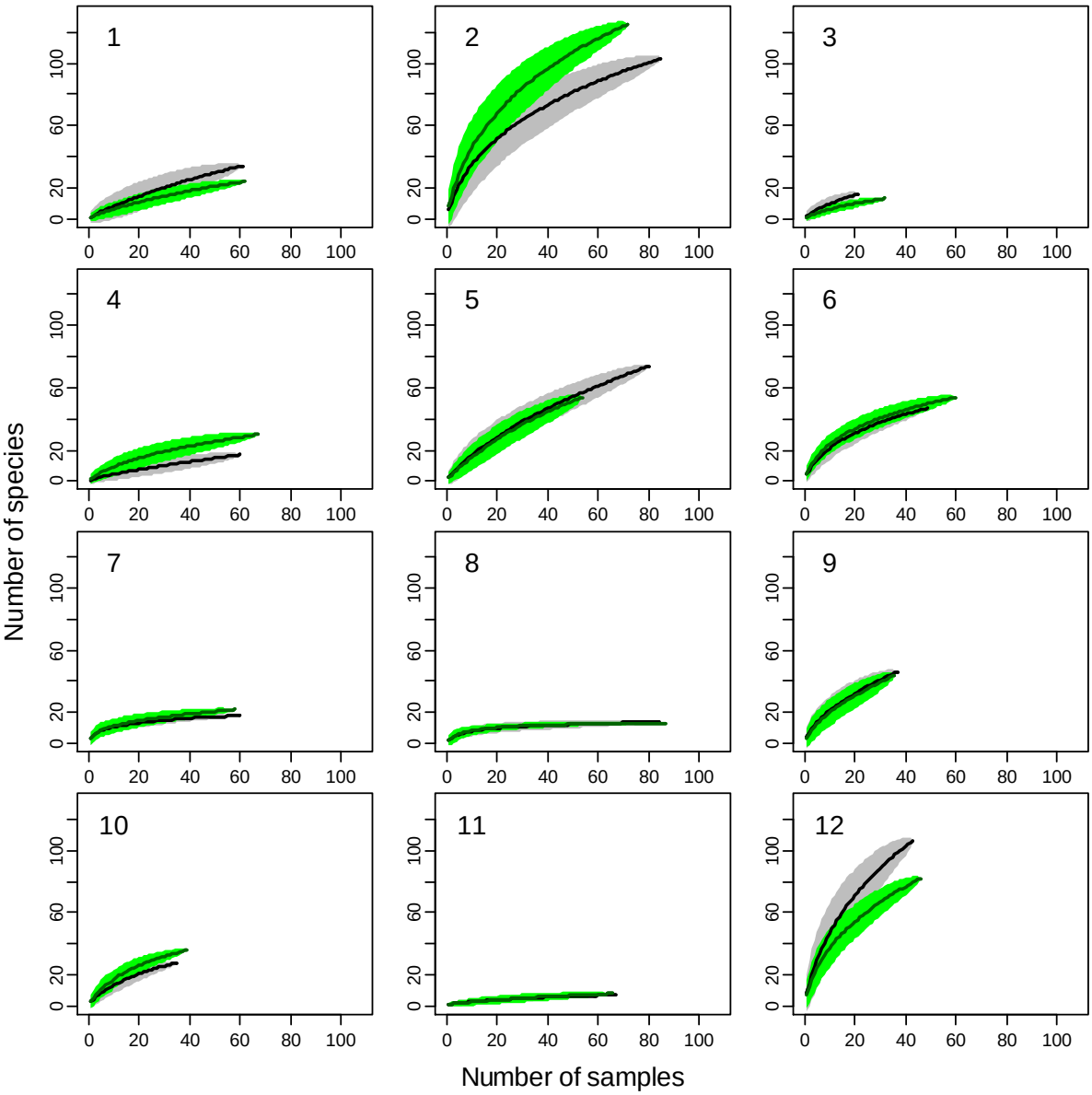

Fig. S4: Bee species accumulation under organic and non-organic farming in twelve regions. Accumulation of the number of bee species with the number of samples in organic (green) and non-organic (grey) fields. Numbers indicate the twelve regions as displayed in Fig. 1a.

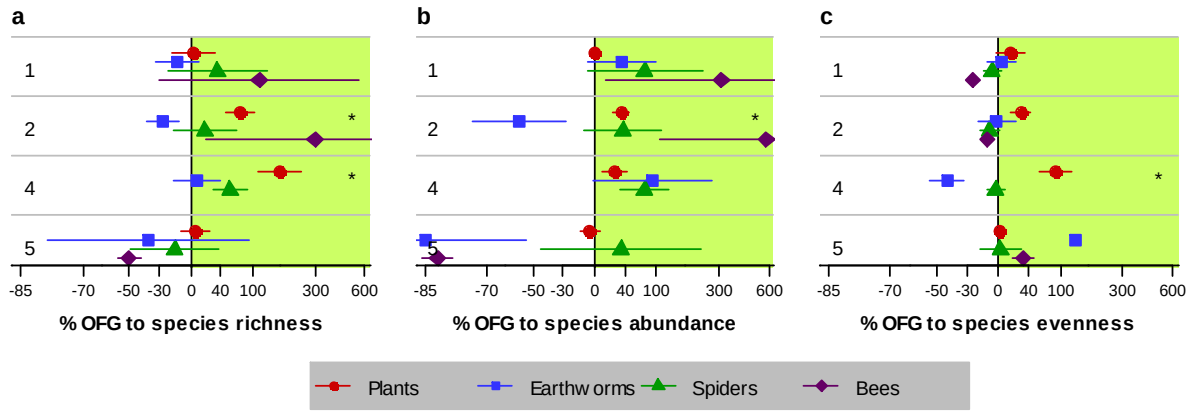

Fig. S5: Organic farming gains and losses (OFG) in the regionally most frequent crops in arable and mixed regions. Organic farming gains/losses (± standard deviation) to species richness (a), organism abundance (b) and species evenness (c) of the four taxonomic groups in the regionally most frequent crop in regions with arable and mixed land use (winter wheat in 1 Marchfeld, 2 Gascony, 4 Southern Bavaria as well as alfalfa in 5 Homokhátság). Effects on bees in Southern Bavaria could not be calculated because no bees were found in non-organic winter wheat fields. X-axis is log-scaled to equalize distances on both sides of parity. Significant differences within regions (U-Test) at 0.05, 0.01, and 0.001% are indicated by *, **, and ***, respectively.

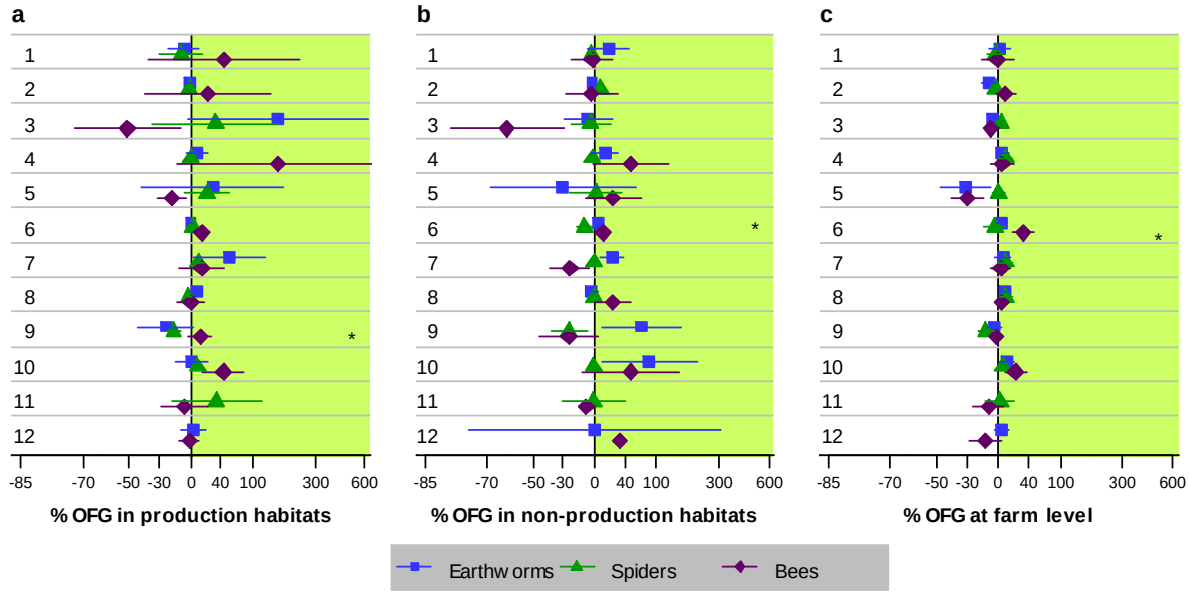

Fig. S6: Organic farming gains and losses (OFG) to rarefied faunal species richness in twelve regions. Organic farming gains/losses (± standard deviation) to rarefied species richness of the three faunal groups in the regionally most frequent production habitats (a), and non-production habitats (b), and on total organism abundance per farm for the faunal groups (c). X-axis is log-scaled to equalize distances on both sides of parity. Significant differences within regions (U-Test) at 0.05, 0.01, and 0.001% are indicated by *, **, and ***, respectively. Numbers indicate the twelve regions as displayed in Fig. 1a
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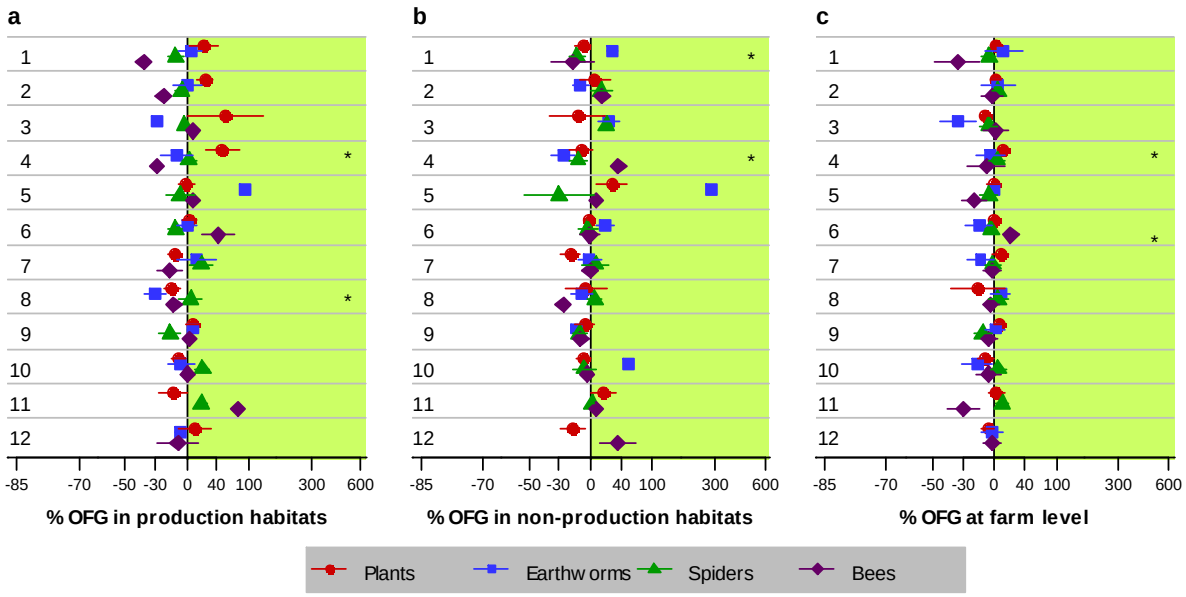

Fig. S7: Organic farming gains and losses (OFG) to species evenness in twelve regions. Organic farming gains/losses (± standard deviation) to species evenness for the four taxonomic groups of plants, earthworms, spiders, and bees in the regionally most frequent production habitats (a), non-production habitats (b) and at farm level (c). X-axis is log-scaled to equalize distances on both sides of parity. Significant differences within regions (U-Test) at 0.05, 0.01, and 0.001% are indicated by *, **, and ***, respectively. Numbers indicate the twelve regions as displayed in Fig. 1a.

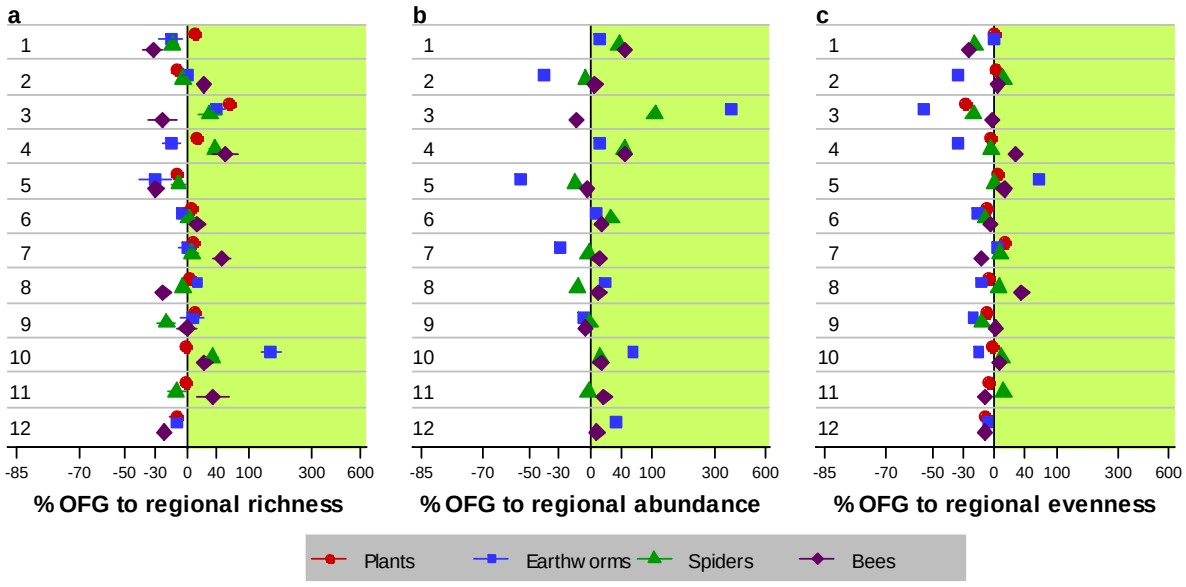

Fig. S8: Organic farming gains and losses to species diversity at regional level. Organic farming gains/losses (± standard deviation) to extrapolated regional species richness using first-order jackknife (a), regional abundance (b), and regional species evenness (c). Regional organism abundance was only calculated for faunal groups. Since only point estimates were available for organism abundance and species evenness, standard deviation could not be calculated. X-axis is log-scaled to equalize distances on both sides of parity. Numbers indicate the twelve regions as displayed in Fig. 1a.

CHAPTER 4

Appropriate Metrics to Inform Farmers about Species Diversity

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Abstract

Farmers are key players in actions to halt biodiversity loss from farmland. However, if farmers are to sustain biodiversity, they must first be adequately informed about biodiversity and understand its drivers. Measuring biodiversity at the farm scale is difficult because of the structural complexity of many farms, and because different aspects of diversity can be considered desirable, e.g. species richness or rarity. In this study we examined 19 grassland farms in Central Switzerland, and sampled plants, earthworms, spiders and bees using a stratified sampling design. We considered several metrics of species diversity, but found two particularly useful at farm scale: average richness (area-weighted) and farm uniqueness in terms of species identity. Average richness reflects the expected species richness in a random sample taken on the farm, and farm uniqueness is the contribution of a farm to the total species richness of all farms under study. Average richness and farm uniqueness are complementary and reflect different aspects of biodiversity. We demonstrate how combining these metrics enables tailored recommendations for enhancing species diversity on the farm.

Keywords

Plant, Earthworm, Spider, Bee, Agricultural management, Farmland habitat

1. Introduction

Agriculture is the main land use in Europe and around 50% of wildlife species are linked to farm habitats (Kristensen, 2003). Changes to these habitats through agricultural intensification have caused populations of many farmland species to decrease critically (Benton et al., 2003), and this loss can impair important ecological functions (Hooper et al., 2005). To remedy this situation, new financial incentives for biodiversity-friendly farming have been introduced into agricultural policy. However, when evaluated, the measures implemented so far have only been partly successful (ECA, 2012; Kleijn et al., 2006). On the one hand, this may be due to ecological reasons. The measures were beneficial, e.g. for certain taxonomic groups but not for rare species (Aviron et al., 2009) or in simple landscapes but less so in complex ones (Batáry et al., 2011). In addition, processes require time until effects can be observed. On the other hand, farmers tend not to give priority to such measures even with financial incentives (Siebert et al., 2006). They may hesitate to implement measures that are imposed by authorities because of entrepreneurship infringement and administrative overload (Clark and Murdoch, 1997). However, the majority of farmers appreciate nature, sense an environmental stewardship and see advantages of ecological functions supplied by biodiversity for their work, e.g. soil fertility, pollination and biological control of pests (Sullivan et al., 1996). Biodiversity is also often associated to other natural resources such as water, soil and air of which farmers acknowledge the need of protection (Fischer and Young, 2007). A dialogue between farmers and researchers on biodiversity was shown to be much more promising than a top-down strategy with excessive control by authorities (Siebert et al., 2006). Farmers generally have a comprehensive view on their land and know how habitats develop and react to agricultural management. In contrast, researchers survey populations of little noticed organisms and assess their contribution to the ecological network. Cooperative approaches hence value the local knowledge of farmers about their land and the environment, as well as scientific evidence in a way that they are useful in agricultural practice.

Farmers are generally experienced at making complex decisions by weighting up multiple sources of external information. This can be the expected market price, cost of machinery and labour, which farmers combine with their personal experience and spatial and climatic constraints to decide on farm structure and management practices (Ahnstrom et al., 2009; Brady et al., 2012; Kelemen et al., 2013). We assume that if better quantitative information about biodiversity, its underlying drivers and its benefits was provided to farmers, they would integrate such information into their management decisions (Home et al., 2014). Therefore, we explore ways of summarizing this quantitative information by appropriate metrics of species diversity.

Selecting robust metrics of species diversity on farms presents a number of substantial challenges. (i) The metrics must be simple, transparent and easy to communicate to farmers and other stakeholders. (ii) Farmers should be able to compare their farm with colleagues' farms and assess their relative performance. They also need to know how management practices are linked to species diversity so that they can enact appropriate measures. (iii) Species diversity has multiple aspects. Goals might be to promote as many species as possible and to preserve rare species (Gaston, 1996). Given that a comprehensive assessment of species diversity at the farm level is not feasible, a single metric is unlikely to be sufficient (Büchs, 2003b). (iv) Farms are economic rather than ecological units and they differ in size and spatial arrangement. Farms include areas directly managed for production and other habitats such as field edges or hedgerows, which are managed by farmers but without the direct aim of production. An appropriate metric should be applicable at the whole-farm scale and therefore needs to rely on stratified sampling to provide adequate coverage of different habitats (Kindt and Coe, 2005). To sum this up, important criteria to select metrics are that they are easy to understand, comparable among farms, and that they are adapted to the levels of biodiversity and to the complexity of farm structures.

In this study, we investigated whether two complementary metrics of species diversity satisfy the criteria outlined above. We assessed the diversity of four contrasting taxonomic groups, i.e. plants, earthworms, spiders and bees, in a mountainous region in Central Switzerland consisting of grassland-based farms. The four taxonomic groups were selected because they are involved in a range of ecological services and occupy different trophic levels. Due to their different mobility and life strategies, they also potentially indicate both, short- and long-term changes of the environmental conditions. The metrics are (1) the average number of species observed in the different habitats of the farm, weighted by the area of these habitats (after Tasser et al., 2008), and (2) the uniqueness of the farm with respect to the species occurrences in the region (after Wagner and Edwards, 2001). Each farm was positioned relative to the regional average of richness and uniqueness of the four taxonomic groups.

2. Methods

2.1. Data Collection

2.1.1. Study Region and Farms

The study region covered 12 km^2 and was located in Central Switzerland, in the Northern Swiss Alps (46°54'N, 8°12'E). The mean annual temperature in the region is 5.6°C, and the average annual precipitation is 1300 mm. The majority of land is grassland for dairy production and breeding. Average slope of farmland is 28%, and 90% of the fields have slopes between 11% and 50%. Soils consist of flysch, sandstones and shale. Of the 66 farms in the region, 19 were randomly selected for the investigation presented here: ten of these were under organic and nine under non-organic management. The farms were located between 605 and 1133 m asl (Arndorfer et al., 2010) and ranged in size between 4 and 20 hectares (on average 10 hectares). The farm unit was defined as the total utilized agricultural area, which included unfarmed habitats such as hedgerows and small copses <800 m^2. Farm buildings, private gardens and forests >800 m^2 were excluded.

2.1.2. Habitat Mapping and Species Sampling

Habitats on each farm were distinguished based on Raunkiær plant life forms, environment and management (Bunce et al., 2008; Raunkiær, 1934). We mapped both areal (at least 5 m wide and covering 400 m^2) and linear habitats (at least 0.5 m wide and 30 m long). We identified 19 different habitat types (12 areal habitat types, 7 linear habitat types; see Appendix A in Supplementary material), and we then surveyed one randomly-selected example of each habitat type on each farm. In total, 139 habitats (4 – 12 habitats per farm) were surveyed (Fig. 1).

In each selected habitat, we sampled species of the four taxonomic groups: plants, earthworms, spiders and bees (wild bees and bumblebees) from spring to early autumn 2010 (Dennis et al., 2012). Plant surveys were conducted on 10 m × 10 m squares for areal habitats and 1 m × 10 m plots for linear habitats. We recorded all species and estimated their respective cover. Earthworms were collected at three random locations per habitat by pouring a solution of allyl isothiocyanate (0.1 g/l) into a metal frame of 30 cm × 30 cm to encourage earthworms to the surface. Subsequently, we sorted a 20 cm deep soil-core by hand. Identification and counting of earthworm species was conducted in the lab. Non clitellates (juveniles and sub-adults) were excluded from the analysis. Spiders were sampled at three dates during the season on five circular areas of 35.7 cm diameter per habitat using a modified leaf blower to suck the spiders from the surface. The samples were frozen on the spot and adults were identified in the lab. Bees were captured during good weather conditions - i.e. during periods of sunshine when it was not too windy and the temperature was higher than 15°C - on three dates with a handheld net along a 100 m x 2 m transect for 15 min. Honeybees (*Apis mellifera*) were excluded from the analysis. Species of all four taxonomic groups were identified to the species level by specialists.

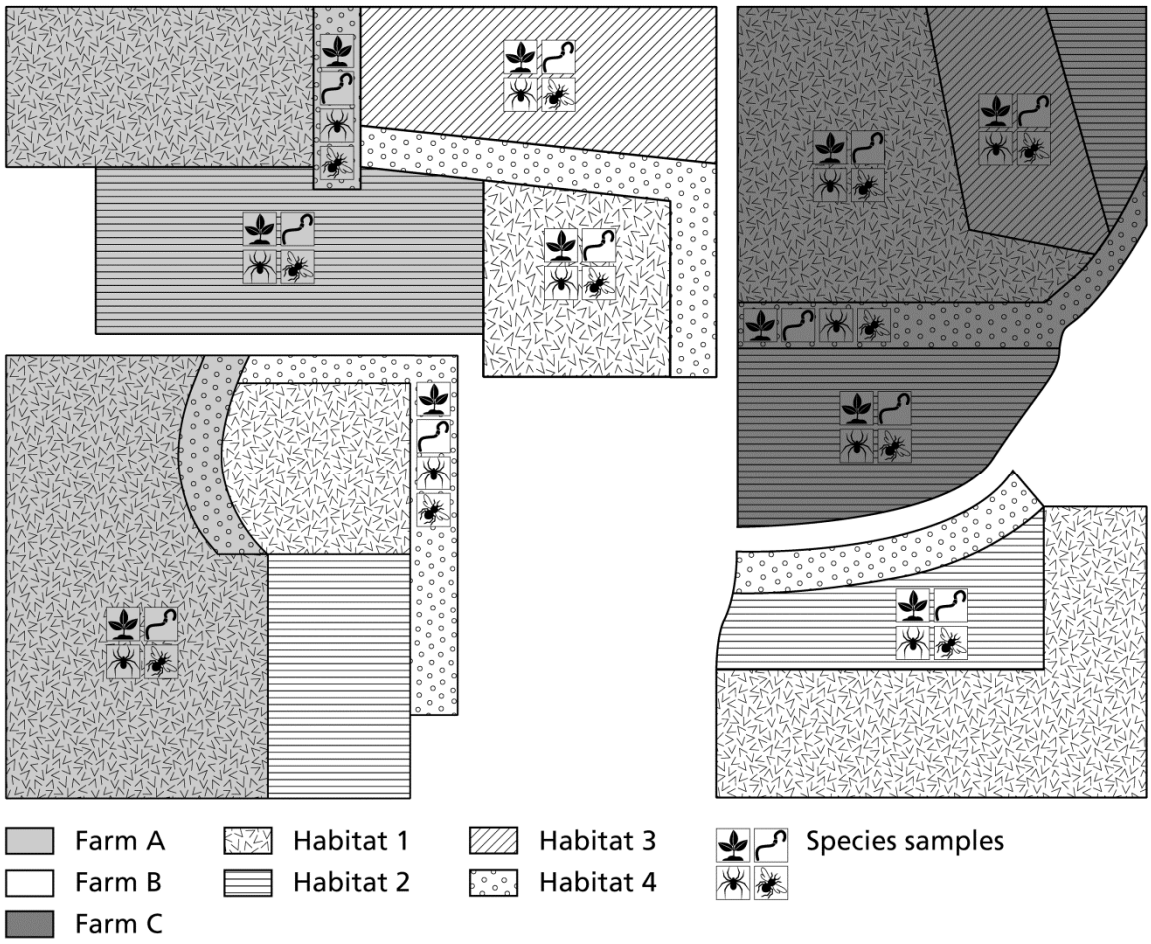

Fig. 1: Schematic representation of the sampling design for three exemplary farms. Farms are indicated by different shading. Each farm consists of different habitat types, indicated by different fill patterns. Species symbols indicate the randomly selected fields where plant, earthworm, spider and bee species were sampled.

2.1.3. Information about Farms, Management Practices and Habitat Characteristics

Farmers were informed about the study and invited to participate by letter and phone calls or personal meetings. During a first visit on the farm, they explained the configuration of the farm to provide a basic matrix for the habitat mapping. After the field work, information of management practices in all habitats investigated was collected in face-to-face interviews with farmers, lasting 1.5 – 3 h. The interviews followed a standardized questionnaire and focused on management frequencies, inputs and general farm characteristics. Out of this information, we calculated management variables at the farm scale (e.g. the average nitrogen input per hectare). Farmers' motivation and attitudes regarding biodiversity were not recorded. Further,

data from the habitat mapping were used to calculate farm-specific habitat characteristics such as the number of areal habitat types or the average habitat size (Herzog et al., 2012).

2.2. Calculation of Average Richness per Farm and Farm Uniqueness

The average richness of the *j*th farm (*AR*) was calculated as

$$AR_j = \sum_h R_{hj} * \frac{A_{hj}}{A_j} \quad (1)$$

where R_{hj} is the number of species found in the sampled habitat of type h (h = 1, 2, …, n_j) in farm j (j = 1, 2, ..., 19). A_{hj} is the sum of the area of all habitats of type h in farm j and A_j is the total area of farm j.

The uniqueness of the *j*th farm (*FU*) was calculated as

$$FU_j = \sum_i \frac{\omega_j \overline{x_{hij}}}{\sum_j \omega_j \overline{x_{hij}}} \quad (2)$$

where $\overline{x_{hij}}$ is the mean abundance of species i in farm j per habitat type h on the farm j, and ω_j is the number of habitat types in farm j, n_j, divided by the total number of habitats sampled in the study area (Wagner and Edwards, 2001; see Appendix B in Supplementary material for an example of the calculation for three farms). In addition to the original reference, we added the term h to Eq. (2) for analogy to Eq. (1).

2.2.1. Normalization of Average Richness and Farm Uniqueness

To provide values of average richness and farm uniqueness that are comparable among different taxonomic groups, we divided each metric by the arithmetic mean across all farms.

For each taxonomic group per farm, average richness and farm uniqueness were first calculated separately. We then calculated the mean average richness over the four taxonomic groups per farm and the mean farm uniqueness over the four taxonomic groups per farm.

Finally, the total mean was the average of the mean average richness and the mean farm uniqueness per farm.

2.3. Data Analysis

We conducted all data analyses with R 2.15.3 (R Development Core Team, 2012).

2.3.1. Correlations and Clustering

To assess the degree to which our two metrics, average richness and farm uniqueness, provide the same information, we correlated these values across farms. Therefore, we first assessed correlations between average richness and farm uniqueness for each taxonomic group in turn, and then assessed correlations between the four taxonomic groups within average richness and farm uniqueness, respectively.

Further, we conducted a cluster analysis to allocate farms to three groups with similar characteristics regarding mean values of average richness and farm uniqueness per taxon, and the total mean over all four taxonomic groups. Partitioning around medoids (R package cluster 1.14.3), which is a robust method of unsupervised divisive classification, was applied. The result was in agreement with the visual consultation of a non-metric multidimensional scaling using vegan 2.0-6.

2.3.2. Regression Analyses

Linear regression was used to explain average richness and farm uniqueness. In order to avoid problems of collinearity, a subset of all available explanatory variables was selected based on ease of interpretation and low variance inflation factors (Borcard et al., 2011). Five of the ten selected variables described management practices: the management system (organic vs. non-organic), the average stocking rate per hectare forage area, total expenditures (on fertiliser, crop protection and concentrate feed stuff), the average nitrogen input per hectare (nearly exclusively organic nitrogen) and the average number of mechanical operations. The other

five explanatory variables described habitat characteristics of the farm: the number of different areal habitat types, the number of different linear habitat types, the average habitat size, the length of linear elements containing woody structures per hectare of farm area and the Shannon diversity index of the habitats per farm. All these explanatory variables were meaningful because farmers are able to influence them (e.g. more or less intensive use of certain habitats, creating or removing new habitats such as hedgerows).

Since both metrics, average richness and farm uniqueness, of the four taxonomic groups satisfied the normality assumption for residuals, linear regression models were estimated with ordinary least squares. Model selection was undertaken using Akaike's information criterion corrected for small samples (Burnham and Anderson, 2002). The significance of effects was assessed using likelihood-ratio tests. Interactions among the explanatory variables were tested, but they did not improve the model fit.

2.4. Calculation of Average Richness per Habitat Category and Habitat Uniqueness

Because of their sparsity within farms, habitats had to be aggregated into four broad categories in order to make comparisons at habitat level useful. The categories were: intensively managed areal habitats (e.g. frequently fertilized and cut grassland), low-input areal habitats (e.g. dry meadows), herbaceous linear habitats (e.g. unpaved tracks) and linear habitats with woody structures (e.g. hedgerows). Detailed information on the grouping is provided in Appendix A, in Supplementary material S.1. Traditionally managed orchards were included in the category intensively managed areal habitats as they were mainly on intensive grassland. For each habitat category, we calculated average richness and habitat uniqueness using equations 1 and 2 (with j = 1, ..., 4 being the habitat categories). To allow comparisons between taxonomic groups, we normalized average richness and habitat uniqueness per habitat category.

3. Results

In 139 sampled habitats on 19 farms, we found 280 plant species, 16 earthworm species (2975 adult individuals), 133 spider species (2802 adult individuals) and 65 wild bee and bumblebee species (763 individuals). The number of species found in a single habitat varied with taxonomic group. For plants the number of species per habitat ranged from 9 to 70 (mean = 34); earthworms ranged from 1 to 10 (mean = 6); spiders ranged from 3 to 20 (mean = 8) and bees ranged from 0 to 10 (mean = 4).

3.1. Evaluation of Average Richness per Farm and Farm Uniqueness

Average richness and farm uniqueness were uncorrelated for the majority of taxonomic groups except for plants, where a significant correlation was found (Table 1). Generally, farms showed different rankings for the four taxonomic groups and this was reflected in missing correlations between the groups. An exception was the positive correlation between the farm uniqueness of plants and bees.

Table 1: Correlations between and within average richness and farm uniqueness. Fields with grey background: correlations between average richness and farm uniqueness for each taxonomic group. Upper panel: correlations between the average richness of the four taxonomic groups. Lower panel: correlations between the farm uniqueness of the four taxonomic groups (*r* = Pearsons's correlation coefficient, *p* = *p*-value). Significant correlations are printed in bold.

	Plants		Earthworms		Spiders		Bees	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Plants	**0.483**	**0.036**	-0.247	0.307	0.311	0.195	0.241	0.320
Earthworms	0.427	0.068	0.158	0.517	-0.396	0.093	0.104	0.671
Spiders	0.447	0.055	0.116	0.638	0.104	0.672	0.032	0.896
Bees	**0.651**	**0.003**	0.264	0.275	0.095	0.698	0.212	0.382

Normalizing average richness and farm uniqueness allowed comparisons across the four taxonomic groups even when the groups differed substantially in absolute magnitude (Fig. 2a – e). Average richness was less variable among farms than farm uniqueness (Standard deviations of average richness and farm uniqueness were 0.185 and 0.539 for plants, 0.180 and 0.391 for earthworms, 0.202 and 0.465 for spiders and 0.338 and 0.516 for bees, respectively).

Cluster analysis resulted in groups of farms with the following characteristics. One group (Fig. 2; circles around farm letters) consisted of farms with a medium average richness and a low farm uniqueness. These farms were generally habitat-poor (4 – 6 habitats per farm). A second group (Fig. 2; quadrates around farm letters) was average for both metrics. These farms varied in the number of different habitat types (5 – 11). The third group of farms (Fig. 2; diamonds around farm letters) had high values for average richness and for farm uniqueness. Most of these farms had a high number of different habitat types (9 – 12, except farm O with only 7 different habitat types).

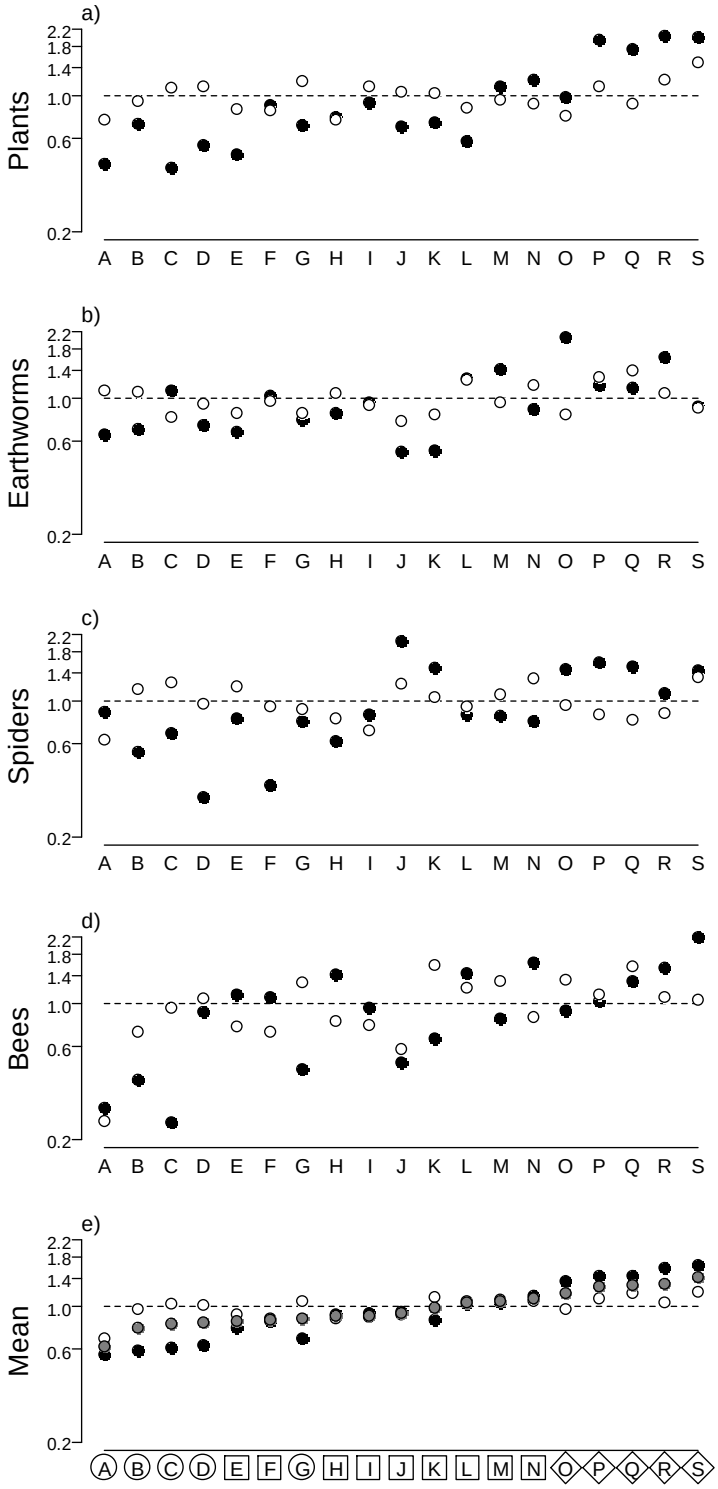

Fig. 2: Species diversity metrics of 19 study farms. Average richness (open circles) and farm uniqueness (filled circles) for (a) plants, (b) earthworms, (c) spiders and (d) bees of farms A to S are shown relative to the average of all 19 farms (dashed line). Panel (e) shows the mean average richness over the four taxonomic groups (open circles), the mean farm uniqueness over the four taxonomic groups (filled circles) and the total mean (grey circles). The *y*-axis is log-scaled to equalize distances below and above the average mean. Farms are ordered according to the total mean. Circles, quadrats and diamonds around farm letters show the grouping of the farms according to a cluster analysis.

3.2. Effects of Management Practices and Habitat Characteristics

Eight out of ten tested explanatory variables had a significant effect on average richness and/or farm uniqueness for at least one taxonomic group (Table 2). No significant effects were found for the length of linear elements with woody structures per hectare and the Shannon diversity index of the habitats.

Average richness of plants and bees were negatively affected by the number of mechanical operations (Table 2a). Average richness of earthworms significantly increased with nitrogen input, the number of areal habitat types and the average habitat size. By contrast, average richness of spiders tended to decrease with the average size of habitats.

Farm uniqueness of plants was significantly increased by the number of different areal habitat types (Table 2b). Farm uniqueness of earthworms was lower on organically managed farms than on non-organically managed farms, and the average stocking rate had a significantly negative effect on farm uniqueness of earthworms. Farm uniqueness of spiders was significantly higher on farms with an increased number of linear habitat types. Farm uniqueness of bees was higher on organically managed farms than on non-organically managed ones. The expenditures (on fertiliser, crop protection and food stuff), the nitrogen input and the average size of habitats had a significant negative effect on farm uniqueness of bees.

The mean average richness over all four taxonomic groups was significantly decreased by the number of mechanical operations (Table 2c). The mean farm uniqueness over all four taxonomic groups and the total mean were both significantly increased by the numbers of areal and linear habitat types.

Table 2: Results of best fitting linear models relating management and habitat variables to (a) average richness, (b) farm uniqueness for plants, earthworms, spiders and bees and (c) the mean average richness and the mean farm uniqueness over all four taxonomic groups and the total mean on 19 farms (Est. = estimated regression coefficient, *p* = *p*-value). Significances are printed in bold.

		Organic vs. non-organic farming		Average stocking rate [LU/ha]		Expenditures [€/ha]		Nitrogen input [kg/ha]		# of mechanical operations		# of areal habitat types		# of linear habitat types		Average size of habitats [ha]		R^2 adjusted of final model
		Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	Est.	*p*	
(a)	Plants									**-0.037**	**<0.001**							0.536
	Earthworms							**0.002**	**0.008**			**0.119**	**<0.001**			**0.00007**	**0.007**	0.598
	Spiders															-0.0001	0.053	0.156
	Bees									-0.039	0.066							0.138
(b)	Plants											**0.262**	**<0.001**					0.701
	Earthworms	**-0.424**	**0.023**	**-0.406**	**0.035**													0.258
	Spiders													**0.236**	**0.002**			0.409
	Bees	**0.488**	**0.010**			**-0.001**	**0.008**	**-0.004**	**0.021**							**-0.0002**	**0.001**	0.658
(c)	Mean average richness[1]									**-0.021**	**0.004**							0.351
	Mean farm uniqueness[1]											**0.110**	**0.002**	**0.117**	**0.008**			0.662
	Total mean											**0.073**	**0.002**	**0.061**	**0.030**			0.619

[1] Over the four taxonomic groups

3.3. Relevance of Habitat Categories

Each of the four aggregated habitat categories had specific importance for the taxonomic groups (Fig. 3). Low-input areal habitats had a high average richness of plants and bees, a high habitat uniqueness of bees and a very high habitat uniqueness for plants. Intensively managed areal habitats were the favourites of earthworm species regarding both metrics. Linear habitats, especially those with woody structures, were the most important for spiders, also regarding both metrics. The means over all four taxonomic groups compensated the differences among the groups. Intensively managed areal habitats were by far the most frequent of the four habitat categories. Despite this, it had the lowest mean average richness ($F = 0.840$, p-value = 0.498) and mean habitat uniqueness ($F = 0.341$, p-value = 0.796). Mean average richness was highest for low-input areal habitats. Mean habitat uniqueness was highest for linear habitats with woody structures.

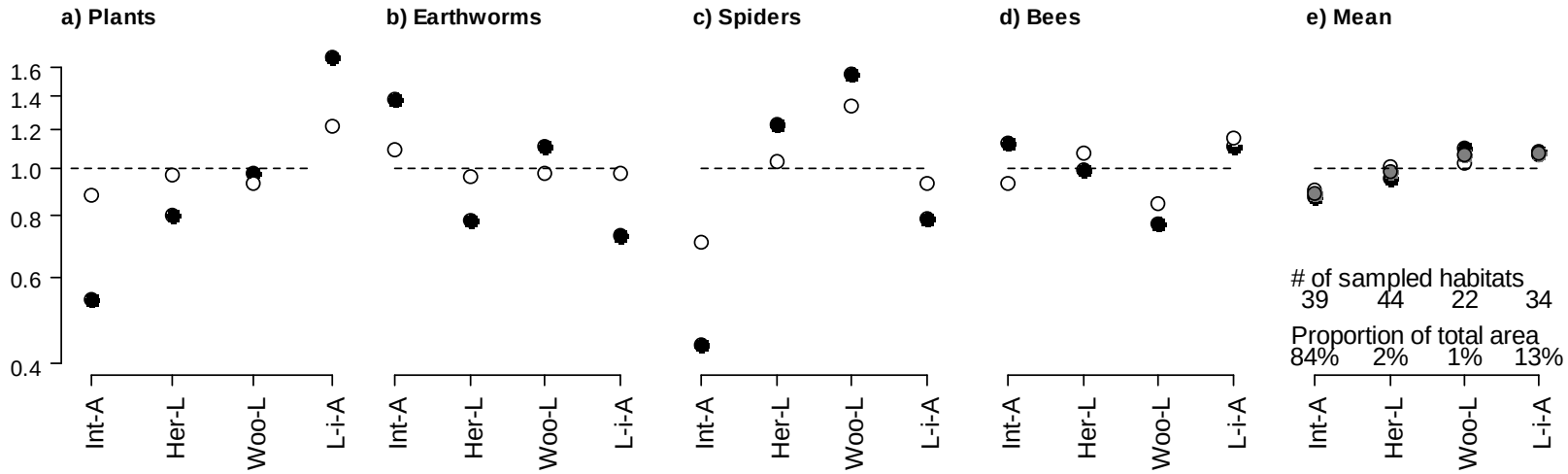

Fig. 3: Species diversity metrics of habitat categories. Average richness (open circles) and habitat uniqueness (filled circles) for (a) plants, (b) earthworms, (c) spiders and (d) bees of four habitat categories: Int-A = intensively managed areal habitats, Her-L = herbaceous linear habitats, Woo-L = linear habitats with woody structures, L-i-A = low-input areal habitats are shown relative to the average of all habitat categories (dashed line). Panel (e) shows the mean average richness over the four taxonomic groups (open circles), the mean habitat uniqueness over the four taxonomic groups (filled circles) and the total mean (grey circles). The *y*-axis is log-scaled to equalize distances below and above the average mean. Habitat categories are ordered according to the total mean.

4. Discussion

4.1. Information about Species Diversity for Farmers

The aim of our study was to devise simple metrics which usefully encapsulate species diversity on farms and supply farmers with quantitative information on biodiversity on their farms. Average richness and farm uniqueness are well-adapted to fulfil most of the criteria postulated in the introduction, namely simplicity, comparability and adaptation to the complexity of biodiversity and farm structures. We propose to provide farmers with an information table on species diversity containing the two farm-level metrics for plants, earthworms, spiders and bees as well as their overall means (Table 3). These eleven values give an amount of information which is easy to overview but still provides some insight into the generating processes (simplicity). The values relate species diversity on the focused farm to species diversity on an average farm in the study region (comparability). The relative nature of the metrics also allows for the assessment of management effects independent of annual fluctuations of populations. Our correlation analysis showed that the two metrics were independent of each other and among the four taxonomic groups (complexity of biodiversity). They convey two aspects of biodiversity: average richness, related to quantity, and farm uniqueness, related to quality. Both aspects are important and should be presented transparently as in Table 3. Finally, the hierarchical assessment method as well as the derived metrics account for the heterogeneity of farm structures (complexity of farm structures). In addition, information may be complemented by the lists of observed species on a farm including their red-list status or other conservational or functional characteristics. Doing so encourages farmers to detect where and why species diversity aspects are well established on their farm and to tap existing potential. We propose to use this information in the context of agricultural consultancy or biodiversity assessments at regional scale.

Table 3: Information on species diversity by the two metrics, average richness and farm uniqueness, of plants, earthworms, spiders and bees and the respective means on three farms of the study region (as example: farm C, H and P, see Fig. 2). Values are given in percentages to the average of the region, i.e. 100%.

Farm	Metric					Mean over the four taxonomic groups	Total mean
C	Average richness	110	80	125	95	103	82
	Farm uniqueness	42	109	68	24	61	
H	Average richness	76	107	82	82	87	89
	Farm uniqueness	77	84	62	143	92	
P	Average richness	112	128	86	112	109	127
	Farm uniqueness	194	118	159	103	144	

4.2. Can General Recommendations for Species Diversity be Derived from Contrasting Taxonomic Groups?

In order to account for the complexity of species diversity, we investigated four contrasting taxonomic groups. Plants, earthworms, spiders and bees differ not only in their food and habitat requirements but also in their mobility. These differences were corroborated by almost independent distributions of the two metrics across the investigated farms, with the exception of farm uniqueness of plants and bees. They also explain contrasting responses to management practices and/or habitat characteristics, which affect diversity metrics of, e.g. earthworms and spiders or earthworms and bees in opposite ways. Nevertheless, our analyses showed that a few variables had consistent positive effects on mean average richness and mean farm uniqueness across all four taxonomic groups. These were primarily a high number of different habitat types and a low management intensity. Current Swiss agricultural policies are partly along these lines in compensating farmers for loss of earnings due to less intensive management (OECD, 2011). Our data suggests that such payments are especially beneficial for plants and bees. Since farm uniqueness of plants tended to be correlated to the farm uniqueness of the other taxonomic groups, plants should be assessed as a priority if only one

group can be inventoried. This finding supports approaches that use plant species as indicators for farm biodiversity due to limited time and financial resources (e.g. SR-910.14, 2001). Indeed, costs of 1006€ were estimated for the assessment of plant diversity on an average farm, applying the methods described above, as compared to 2332, 1993 and 1438€ for earthworm, spider and bee diversity, respectively (Targetti et al., 2014). Nevertheless, many more taxonomic groups than plants depend on farmland and require specific promotion (Büchs, 2003b). For example, as our data showed, spider and bee diversity were promoted by habitat diversity and small-scale heterogeneity. Spiders benefited from linear habitats with a structure-rich vegetation, in line with earlier studies (Gibson et al., 1992; Knop et al., 2006). In addition, small habitat patches contributed significantly to high bee diversity, likely because higher habitat heterogeneity enhanced the chance of continuous food supply and appropriate nesting sites for bees (Kremen et al., 2007). Therefore, creating, maintaining and connecting habitats with structure-rich vegetation and a high flower abundance, will increase species diversity in the study region. This can be best achieved by combining quality assessment and appropriate incentives. In contrast to the other three taxonomic groups, earthworm diversity peaked in the intensively managed areal habitats indicating appropriate soil conditions and sufficient food supply in these grassland fields that nearly exclusively were fertilized with organic nitrogen. Further, deciduous woody habitats contribute considerably to earthworm diversity which was reflected in the high uniqueness of linear habitats with woody structures (Paoletti, 1999a).

4.3. Specific Recommendations to Farmers

Three farms were further scrutinized as representatives for the three groups of farms with specific characteristics, resulting from the cluster analysis. We discuss highlights and potentialities of these farms and make recommendations to enhance species diversity. The information is aimed at being forwarded to the farmers. To be appropriately assimilated by them, communication should be embedded in a familiar environment (Ahnstrom et al., 2009).

We suggest providing the information in individual meetings, preferably on the respective farm. Further, group meetings for farmers of the study region would enable additional exchange of knowledge and practical recommendations (Burton et al., 2008).

Farm C, to begin with, had intermediate average richness across all taxonomic groups but only 61% farm uniqueness of the regional average. This indicated that large areas of this farm mostly contained common species, but the total number of species and/or the number of rare species were low. A closer examination revealed that farm C had only four different habitat types (one intensively managed areal habitat, one low-input areal habitat and two types of grassy linear habitats). To increase its species diversity, farm C should integrate new habitat types, e.g. hedgerows, in order to create new environmental conditions favourable to particular species (Concepción et al., 2012b).

On farm H, both mean average richness and mean farm uniqueness over the species groups were close to the average (87% and 92%, respectively). However, while the average richness and farm uniqueness of plants, earthworms and spiders were close or below the average, farm uniqueness of bees was strikingly high (143%). This can be explained by the presence of a steep meadow with several patches of bare ground and intensive insolation, which was attractive for many ground-nesting bees and their cuckoo bees. The conservation of this habitat is crucial for the farm's bee diversity. Moreover, our data suggest a reduction of mechanical field operations to enhance plant average richness.

The mean average richness and the mean farm uniqueness of farm P were above average. This was mainly due to the very high farm uniqueness of plants (194%) and the high farm uniqueness of spiders (159%). These two taxonomic groups benefited from the high number of different habitat types on this farm. However, the lower average richness of plants and spiders and the high average richness and farm uniqueness of earthworms indicated relatively high management intensity and large habitat patches. Knop et al. (2006) found that a

reduction of mechanical field operations, e.g. a lower cutting frequency and a staggered cutting benefited species diversity. Such management changes are expected to be beneficial for species diversity on farm P, too.

4.4. Contribution to Biodiversity Promotion on Farms by Providing Scientific Information

Providing information about species diversity on farms is one essential step to promote biodiversity on farmland (Home et al., 2014). However, delivering information alone is not sufficient for a fundamental shift in farmland management priorities. To halt the loss of biodiversity in farmland, the cooperation of numerous actors (e.g. authorities, consumers, marketers, farmers or scientists) is crucial (Moon et al., 2012; Siebert et al., 2006). As farmers are key players in their sphere of influence, they have to be involved in knowledge exchange first of all (Burton et al., 2008; Greiner and Gregg, 2011). Scientists have different approaches to and perspectives for biodiversity than farmers (Clark and Murdoch, 1997). Scientists are engaged in detecting secrets in the fascinating diversity of life and rising awareness for the intrinsic value of biodiversity. They may assess the monetary and non-monetary values of ecological functions provided by biodiversity, and reveal the importance of ecosystem services such as soil fertility, pollination and biological control of pests. Hence, scientists can provide recommendations for a collaborative solution process by emphasizing aspects of biodiversity that play a key role for agriculture. We see a high potential for improving the effectiveness of existing recommendations and policies for biodiversity-friendly management if scientists succeed in better informing farmers about biodiversity on their land. The two metrics of species diversity proposed here aim at highlighting the biodiversity “hot spots” on farms and at motivating farmers to promote biodiversity. Such concrete metrics are needed, more than top-down enacted measures, to generate interest and motivate changes in agricultural practices (Burton and Schwarz, 2013). Hence, the next step includes the development and implementation of an attractive communication concept for the two metrics.

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Appendix A and B. Supplementary Material

Appendix A

Table S.1: Distinction of habitats based on primary life forms, environment and management observed directly in the field. Int-A = intensively managed areal habitats, Her-L = herbaceous linear habitats, Woo-L = linear habitats with woody structures, L-i-A = low-input areal habitats.
* Classification in different habitat categories based on precise management information.

Habitat type	Number	Areal/Linear	Habitat category
Grasses and herbs on mesic, eutrophic soil	37	areal	Int-A/L-i-A *
Traditional orchard	8	areal	Int-A
Grasses and herbs on mesic, neutral soil	7	areal	L-i-A
Grasses and herbs on mesic, eutrophic soil; 1 – 10% tree cover	6	areal	Int-A
Grasses and herbs on dry, eutrophic soil	5	areal	L-i-A
Herbs (at least 70% of cover) on mesic, eutrophic soil	4	areal	Int-A/L-i-A *
Grasses (at least 70% of cover) on mesic, eutrophic soil	1	areal	Int-A
Grasses (at least 70% of cover) on mesic, neutral soil	1	areal	L-i-A
Grasses (at least 70% of cover) on wet, eutrophic soil	1	areal	L-i-A
Grasses and herbs on mesic, acid soil; 1 – 10% tree cover	1	areal	L-i-A
Grasses and herbs on wet, eutrophic soil	1	areal	L-i-A
Shrubs (0.05 – 0.3 m)	1	areal	L-i-A
Herbaceous strip	29	linear	Her-L
Species poor hedgerow	12	linear	Woo-L
Private roads and tracks with herbaceous verges	9	linear	Her-L
Species rich hedgerow	9	linear	Woo-L
Grassy strip	4	linear	Her-L
Unpaved tracks	2	linear	Her-L
Line of trees	1	linear	Woo-L

Appendix B

Table S.2: Example for the calculation of the farm uniqueness of three farms. (a) Number of observations of species *i* in farm *j* and the number of habitat types in farm *j*, (b) The mean number of observations of species *i* per habitat type in the farm and weight of the farm proportional to its number of habitat types (ω_j); (c) Weighted mean number of observations of species per farm and sum of them per species; (d) Specificity of species *i* to farm *j* ($\sum_j \omega_j \overline{x_{hij}}$) and uniqueness of farm *j* ($FU_j = \sum_i \frac{\omega_j \overline{x_{hij}}}{\sum_j \omega_j \overline{x_{hij}}}$, Wagner and Edwards, 2001).

(a)	Sp 1	Sp 2	Sp 3	Sp 4	Sp 5	# of habitat types (in farm)
Farm A	9	5	2	1	1	3
Farm B	3	3	0	2	0	2
Farm C	10	7	4	0	5	4

(b) $\overline{x_{hij}}$	Sp 1	Sp 2	Sp 3	Sp 4	Sp 5	ω_j
Farm A	3.000	1.667	0.667	0.333	0.333	0.333
Farm B	1.500	1.500	0.000	1.000	0.000	0.222
Farm C	2.500	1.750	1.000	0.000	1.250	0.444

(c) $\omega_j \overline{x_{hij}}$	Sp 1	Sp 2	Sp 3	Sp 4	Sp 5
Farm A	1.000	0.556	0.222	0.111	0.111
Farm B	0.333	0.333	0.000	0.222	0.000
Farm C	1.111	0.778	0.444	0.000	0.556
$\sum_j \omega_j \overline{x_{hij}}$	2.444	1.667	0.667	0.333	0.667

(d)

$\frac{\omega_j \overline{x_{hij}}}{\sum_j \omega_j \overline{x_{hij}}}$	Sp 1	Sp 2	Sp 3	Sp 4	Sp 5	$FU_j = \sum_i \frac{\omega_j \overline{x_{hij}}}{\sum_j \omega_j \overline{x_{hij}}}$
Farm A	0.409	0.333	0.333	0.333	0.167	1.576
Farm B	0.136	0.200	0.000	0.667	0.000	1.003
Farm C	0.455	0.467	0.667	0.000	0.833	2.421
Sum						5

GENERAL DISCUSSION

Investigating biodiversity resembles a patchwork of a multitude of studies and insights. Each approach requires clear targets to be set, a weighing up of effort and limitations, and an assessment of the experiences to be gained. Such information allows further steps to be identified for the advancement of biodiversity knowledge. Here, I discuss three points that were found in this study to be meaningful for in this context: (1) the role of four contrasting taxonomic groups as a subset of species diversity, (2) indirect assessments of species diversity and (3) the potential of taking into account different spatial scales.

1. Four Contrasting Taxonomic Groups as a Subset of Species Diversity

Within this study, vascular plant, earthworm, spider and bee (wild bee) communities were examined as components of biodiversity in farmland. The four taxonomic groups were representative of different trophic levels, i.e. primary producers, decomposers, predators and pollinators, and altogether, they covered a broad spectrum of species diversity. As each group responded individually to the tested explanatory variables, the study showed that human activities and surrounding landscapes characteristics differently affect components of species diversity. Correlations between taxonomic groups were rare (Table 5 in Chapter 1 and Table S10 in Chapter 2), indicating that the consideration of contrasting groups enhances the knowledge on overall species diversity. In detail, the most significant correlations were found between plants and bees, because bees directly rely on plants as food resource. Presumably, the consideration of plant traits related to pollen and nectar availability or the flowering status would have resulted in even more and stronger correlations. In addition, the number of significant correlations was higher between plants, which are the organisms at the basis of the whole food web, and earthworms, spiders or bees, respectively, than between two of the faunal groups. Thus, our results are in line with previous studies on cross-taxon congruence. Although some studies have suggested surrogate taxa for biodiversity assessments based on

cross-taxon congruence (e.g. Sauberer et al., 2004), most emphasize that careful selection of spatial extent and community aspects is necessary if single taxa are to be used to draw conclusions relating to general biodiversity (Lund and Rahbek, 2002, Su et al., 2004, Oertli et al., 2005).

2. Indirect Assessments of Species Diversity

The assessment of species diversity as it was undertaken here, directly addressed a crucial level of biodiversity. Such detailed information is highly relevant. However, there is a trade-off between costs and quality, as well as quantity of data collection. A second challenge is mainly relevant in the context of farmland biodiversity, where results may have implications for policy and farmers. Therefore, communication of results can be both detailed and specific, as well as more generalised so that it is easy and quick to understand. An example of a simplification is to use known effects of agricultural management on species diversity for indirect assessments based on management information (e.g. Jeanneret et al., 2008). Such assessments should be applied with caution to regions where knowledge on relations between agricultural management and species diversity is rare. This is because effects of agricultural management on plant, earthworm, spider and bee communities was found to be highly variable among regions in this study. Nevertheless, in arable fields, the effects of agricultural management on plant, spider and bee communities were independent of geographic location (Fig. 2 in Chapter 1). Namely mineral fertilization and pesticide applications decreased species diversity. In grassland fields, agricultural management explained less of the variation in all communities. In contrast to the arable fields, the surrounding landscape characteristics had more distinct effects (Fig. 2 in Chapter 2). For the up-scaling of species diversity measurements from field to farm scale, both, productive fields and semi-natural habitats, were considered. This indicated that effects of agricultural management were to a lesser extent reflected in species diversity at farm scale than at habitat scale (Fig. 2 in Chapter 3). Thus,

indirect assessments of biodiversity via agricultural management or habitat characteristics remain useful for rough estimations but need an ongoing adaptation based on direct findings.

3. The Potential of Analyses at Different Spatial Scales

The stratified sampling design applied in the BioBio project to assess species diversity was appropriate for a farm scale approach based on habitat surveys. Although farm scale is not an ecologically meaningful scale, it is the scale where crucial decisions regarding biodiversity in farmland are taken. The step from species diversity at habitat scale to species diversity at farm scale bore major challenges which was e.g. identified in the comparison of species diversities in organic and in non-organic farms. Normally, entire farms are managed either according to the criteria of organic farming or not. And indeed, most of the farmed area was highly influenced by management. However, additional area was classified as semi-natural habitat. Our study showed that these semi-natural habitats on non-organic farms partly compensated for the benefit of organic farming in intensively managed habitats on species diversity. Therefore, decisions that were made at farm scale were relevant for certain habitats, but its effect faded when the whole farm was considered. This issue was taken into account when providing metrics to inform farmers on species diversity in their sphere of influence. The suggested metrics, average richness (area-weighted) and farm uniqueness to describe plant, earthworm, spider and bee diversity at farm scale enable closer adherence to the actual data and avoid more abstract score or point systems. They provide an overview of the farm's value regarding species diversity. Diversity metrics provide relative rather than absolute values (Gaston 1996). Therefore, the suggested metrics are meaningful for comparisons of farms within the same study region, independent of their spatial extent and structure. This overview should be used to raise awareness and interest. The next step would then lead back to the habitat scale. Here, the goal would be to deepen understanding, foster communication

between researchers and farmers and find appropriate recommendations that promote species diversity in farmland.

4. Closing Words

To conserve and promote biodiversity, a broad knowledge is indispensable. The measurement and evaluation of plant, earthworm, spider and bee communities in farmland opened a window to the vast amount of creatures growing, flowering, creeping and crawling below, on and above the ground that is dedicated to agricultural production. The great potential of large scale inventories, as presented here, relies crucially on standardized methods and approaches. If results are comprehensible and comparable, new pieces can be added to the existing patchwork of biodiversity exploration. Last but not least, for the effective implementation of new findings, an appropriate communication is needed to awake awareness and interest for the fascinating diversity that still holds numerous secrets.

REFERENCES

Adler, P.B., Seabloom, E.W., Borer, E.T., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W.S., O'Halloran, L.R., Grace, J.B., Anderson, T.M., Bakker, J.D., Biederman, L.A., Brown, C.S., Buckley, Y.M., Calabrese, L.B., Chu, C.J., Cleland, E.E., Collins, S.L., Cottingham, K.L., Crawley, M.J., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Fay, P.A., Firn, J., Frater, P., Gasarch, E.I., Gruner, D.S., Hagenah, N., Lambers, J.H.R., Humphries, H., Jin, V.L., Kay, A.D., Kirkman, K.P., Klein, J.A., Knops, J.M.H., La Pierre, K.J., Lambrinos, J.G., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Mortensen, B., Orrock, J.L., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Wang, G., Wragg, P.D., Wright, J.P., Yang, L.H., 2011. Productivity is a poor predictor of plant species richness. Science 333, 1750-1753.

Ahnstrom, J., Hockert, J., Bergea, H.L., Francis, C.A., Skelton, P., Hallgren, L., 2009. Farmers and nature conservation: what is known about attitudes, context factors and actions affecting conservation? Renew. Agric. Food Syst. 24, 38-47.

Arndorfer, M., Angelova, S., Balázs, K., Bogers, M.M.I., Centeri, C., Choisis, J.-P., Dennis, P., Eiter, S., Falusi, E., Fjellstad, W., Friedel, J.K., Geijzendorffer, I.R., Gomiero, T., Griffioen, A.J., Guteva, Y., Jongman, R.H.G., Juárez, E., Kainz, M., Kelemen, E., Lüscher, G., Mayr, J., Moreno, G., Paoletti, M.G., Podmaniczky, L., Sarthou, J.P., Skutai, J., Stoyanova, S., Schneider, M.K., Siebrecht, N., Wolfrum, S., Wilkes, J., Zanetti, T., 2010. Delimitation of BIOBIO Case Study Regions and the Selection of Case Study Farms. Division of Organic Farming, University of Natural Resources, Applied Life Sciences, Vienna.

Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schupbach, B., Walter, T., Herzog, F., 2009. Ecological cross compliance promotes farmland biodiversity in Switzerland. Front. Ecol. Environ. 7, 247-252.

Báldi, A., Batáry, P., Kleijn, D., 2013. Effects of grazing and biogeographic regions on grassland biodiversity in Hungary - analysing assemblages of 1200 species. Agric. Ecosyst. Environ. 166, 28-34.

Balmford, A., Green, R., Phalan, B., 2012. What conservationists need to know about farming. Proc. R. Soc. B Biol. Sci. 279, 2714–2724.

Banaszak, J., 1980. Studies on methods of censusing the numbers of bees (Hymenoptera, Apoidea). Pol. Ecol. Stud. 6, 355–365.

Batáry, P., Báldi, A., Kleijn, D., Tscharntke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc. R. Soc. B. 278, 1894-1902.

Batáry, P., Báldi, A., Sárospataki, M., Kholer, F., Verhulst, J., Knop, E., Herzog, F., Kleijn, D., 2010. Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. Agric. Ecosyst. Environ. 136, 35-39.

Batáry, P., Holzschuh, A., Orci, K.M., Samu, F., Tscharntke, T., 2012. Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. Agric. Ecosyst. Environ. 146, 130-136.

Batáry, P., Kovács, A., Báldi, A., 2008. Management effects on carabid beetles and spiders in Central Hungarian grasslands and cereal fields. Community Ecol. 9, 247-254.

Bengtsson, J., Ahnstrom, J., Weibull, A.C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. J. Appl. Ecol. 42, 261-269.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182-187.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekotter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., van Wingerden, W., Zobel, M., Edwards, P.J., 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. J. Appl. Ecol. 45, 141-150.

Bohan, D.A., Haughton, A.J., 2012. Effects of local landscape richness on in-field weed metrics across the Great Britain scale. Agric. Ecosyst. Environ.158, 208-215.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer Science+Business Media, New York.

Brady, M., Sahrbacher, C., Kellermann, K., Happe, K., 2012. An agent-based approach to modeling impacts of agricultural policy on land use, biodiversity and ecosystem services. Landsc. Ecol. 27, 1363-1381.

Brandt, K., Leifert, C., Sanderson, R., Seal, C. J., 2011. Agroecosystem management and nutritional quality of plant foods: the case of organic fruits and vegetables. Crit. Rev. Plant Sci. 30, 177–197.

Brito, I., Carvalho, M., Goss, M.J., 2013. Soil and weed management for enhancing arbuscular mycorrhiza colonization of wheat. Soil Use Manage. 29, 540-546.

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J., Potts, S.G., 2010. Impacts of a pesticide on pollinator species richness at different spatial scales. Basic Appl. Ecol. 11, 106-115.

Browne, W.J., Subramanian, S.V., Jones, K., Goldstein, H., 2005. Variance partitioning in multilevel logistic models that exhibit overdispersion. J. R. Stat. Soc. Ser. A Stat. Soc. 168, 599–613.

Büchs, W., 2003a. Biodiversity and agri-environmental indicators - general scopes and skills with special reference to the habitat level. Agric. Ecosyst. Environ. 98, 35-78.

Büchs, W., 2003b. Biotic indicators for biodiversity and sustainable agriculture - introduction and background. Agr. Ecosyst. Environ. 98, 1-16.

Bunce, R.G.H., Bogers, M.M.B., Roche, P., Walczak, M., Geijzendorffer, I.R., Jongman, R.H.G. 2011. Manual for Habitat and Vegetation Surveillance and Monitoring. Alterra report 2154. Wageningen.

Bunce, R.G.H., Metzger, M.J., Jongman, R.H.G., Brandt, J., De Blust, G., Elena-Rossello, R., Groom, G.B., Halada, L., Hofer, G., Howard, D.C., Kovar, P., Mucher, C.A., Padoa-Schioppa, E., Paelinx, D., Palo, A., Perez-Soba, M., Ramos, I.L., Roche, P., Skanes, H., Wrbka, T., 2008. A standardized procedure for surveillance and monitoring European habitats and provision of spatial data. Landsc. Ecol. 23, 11-25.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Burton, R.J.F., Kuczera, C., Schwarz, G., 2008. Exploring farmers' cultural resistance to voluntary agri-environmental schemes. Sociol. Rural. 48, 16-37.

Burton, R.J.F., Schwarz, G., 2013. Result-oriented agri-environmental schemes in Europe and their potential for promoting behavioural change. Land Use Policy 30, 628-641.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J.C., Watson, R. 2010. Global biodiversity: indicators of recent declines. Science, 328, 1164-1168.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissiere, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. Agric. Ecosyst. Environ. 133, 40-47.

Carvell, C., Osborne, J.L., Bourke, A.F.G., Freeman, S.N., Pywell, R.F., Heard, M.S., 2011. Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. Ecol. Appl. 21, 1760-1771.

Chan, K.Y., 2001. An overview of some tillage impacts on earthworm population abundance and diversity - implications for functioning in soils. Soil Tillage Res. 57, 179-191.

Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecol. Lett. 8, 148-159.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45-67.

Chongtham, I. R., de Neergaard, A., Pillot, D., 2010. Assessment of the strategies of organic fruit production and fruit drying in Uganda. J. Agric. Rural Dev. Trop. Subtrop. 111, 23–34.

Chaplin-Kramer, R., Kremen, C., 2012. Pest control experiments show benefits of complexity at landscape and local scales. Ecol. Appl. 22, 1936-1948.

Clark, J., Murdoch, J., 1997. Local knowledge and the precarious extension of scientific networks: a reflection on three case studies. Sociol. Rural. 37, 38-60.

Clough, Y., Kruess, A., Kleijn, D., Tscharntke, T., 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. J. Biogeogr. 32, 2007-2014.

Colwell, R. K., Mao, C. X., Chang, J., 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85, 2717–2727.

Conant, R. T., Berdanier, A. B., Grace, P. R., 2013. Patterns and trends in nitrogen use and nitrogen recovery efficiency in world agriculture. Glob. Biogeochem. Cycles 27, 558–566.

Concepción, E.D., Diaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012a. Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. J. Appl. Ecol. 49, 695-705.

Concepción, E.D., Fernandez-Gonzalez, F., Diaz, M., 2012b. Plant diversity partitioning in Mediterranean croplands: effects of farming intensity, field edge, and landscape context. Ecol. Appl. 22, 972-981.

Costanza, R., D'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van Den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253-260.

Crowder, D. W., Northfield, T. D., Gomulkiewicz, R., Snyder, W. E., 2012. Conserving and promoting evenness: organic farming and fire-based wildland management as case studies. Ecology 93, 2001–2007.

Dennis, P., Bogers, M.M.B., Bunce, R.G.H., Herzog, F., Jeanneret, P., 2012. Biodiversity in Organic and Low-input Farming Systems. Handbook for Recording Key Indicators. Alterra report 2308, Wageningen.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. Science, 344, 269-273.

Drapela, T., Moser, D., Zaller, J.G., Frank, T., 2008. Spider assemblages in winter oilseed rape affected by landscape and site factors. Ecography 31, 254-262.

Duelli, P., Obrist, M.K., 1998. In search of the best correlates for local organismal biodiversity in cultivated areas. Biodivers. Conserv. 7, 297-309.

Duelli, P., Obrist, M.K., 2003. Biodiversity indicators: the choice of values and measures. Agric. Ecosyst. Environ. 98, 87-98.

ECA, 2012. Annual Report on the Implementation of the Budget Concerning the Financial Year 2011.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms. Chapman and Hall, London.

EEA, 2010. Assessing biodiversity in Europe — the 2010 report.

European Commission, Eurostat., 2011. Nitrogen balance in agriculture - Statistics Explained. http://epp.eurostat.ec.europa.eu/statistics_explained/index.php/Nitrogen_balance_in_agriculture#

Fischer, A., Young, J.C., 2007. Understanding mental constructs of biodiversity: implications for biodiversity management and conservation. Biol. Conserv. 136, 271-282.

Fischer, J., Batáry, P., Bawa, K.S., Brussaard, L., Chappell, M.J., Clough, Y., Daily, G.C., Dorrough, J., Hartel, T., Jackson, L.E., Klein, A.M., Kremen, C., Kuemmerle, T., Lindenmayer, D.B., Mooney, H.A., Perfecto, I., Philpott, S.M., Tscharntke, T., Vandermeer, J., Wanger, T.C., Von Wehrden, H., 2011. Conservation: limits of land sparing. Science, 334, 593.

Fried, G., Norton, L.R., Reboud, X., 2008. Environmental and management factors determining weed species composition and diversity in France. Agric. Ecosyst. Environ. 128, 68-76.

Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, A.C., Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald, D.W., Firbank, L.G., 2005. Benefits of organic farming to biodiversity vary among taxa. Biol. Lett. 1, 431-434.

Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V., Petit, S., 2010. Weed species richness in winter wheat increases with landscape heterogeneity. Agric. Ecosyst. Environ. 138, 318-323.

Gabriel, D., Roschewitz, I., Tscharntke, T., Thies, C., 2006. Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. Ecol. Appl., 16, 2011-2021.

Gabriel, D., Sait, S.M., Hodgson, J.A., Schmutz, U., Kunin, W.E., Benton, T.G., 2010. Scale matters: the impact of organic farming on biodiversity at different spatial scales. Ecol. Lett. 13, 858-869.

Gabriel, D., Sait, S.M., Kunin, W.E., Benton, T.G., 2013. Food production vs. biodiversity: comparing organic and conventional agriculture. J. Appl. Ecol. 50, 355–364.

Gabriel, D., Thies, C., Tscharntke, T., 2005. Local diversity of arable weeds increases with landscape complexity. Perspect. Plant Ecol. Evol. Syst. 7, 85-93.

Gaujour, E., Amiaud, B., Mignolet, C., Plantureux, S., 2012. Factors and processes affecting plant biodiversity in permanent grasslands. A review. Agron. Sustain. Dev. 32, 133-160.

Gaston, K.J.H., 1996. Biodiversity: A Biology of Numbers and Difference, 1st ed. Blackwell Science Ltd., Oxford.

Gelman, A., Hill, J., 2006. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press.

Gelman, A., Hill, J., Yajima, M., 2012. Why we (usually) don't have to worry about multiple comparisons. J. Res. Educ. Eff. 5, 189–211.

Gibson, C.W.D., Hambler, C., Brown, V.K., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. J. Appl. Ecol. 29, 132-142.

Gibson, R.H., Pearce, S., Morris, R.J., Symondson, W.O.C., Memmott, J., 2007. Plant diversity and land use under organic and conventional agriculture: A whole-farm approach. J. Appl. Ecol. 44, 792-803.

Gomiero, T., Pimentel, D., Paoletti, M.G., 2011. Environmental impact of different agricultural management practices: conventional vs. organic agriculture. Crit. Rev. Plant Sci. 30, 95–124.

Gorton, M., Douarin, E., Davidova, S., Latruffe, L., 2008. Attitudes to agricultural policy and farming futures in the context of the 2003 CAP reform: a comparison of farmers in selected established and new member states. J. Rural Stud.24, 322-336.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379-391.

Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol. 53, 191-208.

Greiner, R., Gregg, D., 2011. Farmers' intrinsic motivations, barriers to the adoption of conservation practices and effectiveness of policy instruments: empirical evidence from northern Australia. Land Use Policy 28, 257-265.

Grenouillet, G., Pont, D., Seip, K.L., 2002. Abundance and species richness as a function of food resources and vegetation structure: juvenile fish assemblages in rivers. Ecography, 25, 641-650.

Guillem, E.E., Barnes, A., 2013. Farmer perceptions of bird conservation and farming management at a catchment level. Land Use Policy 31, 565-575.

Harker, K.N., O'Donovan, J.T., 2013. Recent weed control, weed management, and integrated weed management. Weed Technol. 27, 1-11.

Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. Nature 448, 188-190.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. Science 286, 1123-1127.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Heltshe, J.F., Forrester, N.E., 1983. Estimating species richness using the jackknife procedure. Biometrics 1–11.

Herzfeld, T., Jongeneel, R., 2012 Why do farmers behave as they do? Understanding compliance with rural, agricultural, and food attribute standards. Land Use Policy 29, 250–260.

Herzog, F., Balázs, K., Dennis, P., Friedel, J., Geijzendorffer, I.R., Jeanneret, P., Kainz, M., Pointereau, P., 2012. Biodiversity Indicators for European Farming Systems. A Guidebook. Forschungsanstalt Agroscope Reckenholz-Tänikon ART, Zürich.

Heywood, V.H., Watson, R.T.H., 1995. -, In: UNEP (Ed.), Global Biodiversity Assessment. Cambridge University Press.

Hinners, S.J., Kearns, C.A., Wessman, C.A., 2012. Roles of scale, matrix, and native habitat in supporting a diverse suburban pollinator assemblage. Ecol. Appl. 22, 1923-1935.

Hodgson, J. A., Kunin, W. E., Thomas, C. D., Benton, T. G., Gabriel, D., 2010. Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. Ecol. Lett. 13, 1358–1367.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, F., Evans, A.D., 2005. Does organic farming benefit biodiversity? Biol. Conserv. 122, 113-130.

Holland, J.M., 2004. The environmental consequences of adopting conservation tillage in Europe: reviewing the evidence. Agric. Ecosyst. Environ. 103, 1-25.

Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J. Anim. Ecol. 79, 491-500.

Home, R., Balmer, O., Jahrl, I., Stolze, M., Pfiffner, L., 2014. Motivations for implementation of ecological compensation areas on Swiss lowland farms. J. Rural Stud. 34, 26-36.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J.,

Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consenus of current knowledge. Ecol. Monogr. 75, 3-35.

Hurlbert, S.H., 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology, 52, 577-589.

Hyvönen, T., Huusela-Veistola, E., 2008. Arable weeds as indicators of agricultural intensity - A case study from Finland. Biol. Conserv. 141, 2857-2864.

Hyvönen, T., Salonen, J., 2002. Weed species diversity and community composition in cropping practices at two intensity levels - a six-year experiment. Plant Ecol. 154, 73-81.

IFOAM, 2012. The IFOAM Norms for Organic Production and Processing. International Federation of Organic Agriculture Movements.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. Nature 477, 199-202.

Jeanneret, P., Baumgartner, D., Freiermuth Knuchel, R., Gaillard, G., 2008. A new LCIA method for assessing impacts of agricultural activities on biodiversity (SALCA-Biodiversity), In: Gaillard, G. (Ed.), Proceedings of the 6th International Conference on LCA in the Agri-Food Sector. ART, Zurich, 34-39.

Jeanneret, P., Schüpbach, B., Luka, H., 2003. Quantifying the impact of landscape and habitat features on biodiversity in cultivated landscapes. Agric. Ecosyst. Environ. 98, 311-320.

Jost, L., 2006. Entropy and diversity. Oikos 113, 14.

Jost, L., 2007. Partitioning diversity into independent alpha and beta components. Ecology 88, 2427-2439.

Khedher, M.B., Nabli, H., 2003. Strategy of organic market in Tunisia. Cah. Options Méditerranéennes 61, 187–190.

Kelemen, E., Nguyen, G., Gomiero, T., Kovács, E., Choisis, J.-P., Choisis, N., Paoletti, M.G., Podmaniczky, L., Ryschawy, J., Jean-Pierre, S., Herzog, F., Dennis, P., Balázs, K., 2013. Farmers' perceptions of biodiversity: lessons from a discourse-based deliberative valuation study. Land Use Policy 35, 318-328.

Kindt, R., Coe, R., 2005. Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agroforestry Centre (ICRAF), Nairobi.

Kleijn, D., Baquero, R.A., Clough, Y., Dıaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243-254.

Kleijn, D., Kohler, F., Baldi, A., Batary, P., Concepcion, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. Proc. R. Soc. B.276, 903-909.

Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., Tscharntke, T., 2011. Does conservation on farmland contribute to halting the biodiversity decline? Trends Ecol. Evol. 26, 474–481.

Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? Journal of Applied Ecology, 40, 947-969.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B. 274, 303-313.

Knop, E., Kleijn, D., Herzog, F., Schmid, B., 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. J. Appl. Ecol. 43, 120-127.

Kovács-Hostyánszki, A., Batáry, P., Báldi, A., Harnos, A., 2011. Interaction of local and landscape features in the conservation of Hungarian arable weed diversity. Appl. Veg. Sci. 14, 40-48.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol. Lett. 10, 299-314.

Kristensen, P., 2003. EEA Core Set of Indicators: Revised Version April 2003. European Environment Agency, Copenhagen.

Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., Burel, F., 2010. Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. Agric. Ecosyst. Environ. 137, 143-150.

Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecol. Monogr. 75, 435-450.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271-280.

Legendre, P., Legendre, L., 2012. Numerical Ecology, Elsevier ed., Amsterdam.

Loreau, M., Naeem, S., Inchausti, P., 2002. Biodiversity and Ecosystem Functioning - Synthesis and Perspectives. Oxford University Press, USA.

Lozano-García, B., Parras-Alcántara, L., 2013. Land use and management effects on carbon and nitrogen in Mediterranean Cambisols. Agric. Ecosyst. Environ. 179, 208–214.

Lund, M.P., Rahbek, C., 2002. Cross-taxon congruence in complementarity and conservation of temperate biodiversity. Anim. Conserv. 5, 163-171.

Lüscher, G., Jeanneret, P., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D., Bernhardt, K.G., Choisis, J.-P., Elek, Z., Frank, T., Friedel, J.K., Kainz, M., Kovács-Hostyánszki, A., Oschatz, M.-L., Paoletti, M.G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S., Herzog, F., 2014. Responses of plants, earthworms, spiders and bees to geographic location, agricultural management and surrounding landscape in European arable fields. Agric. Ecosyst. Environ. 186, 124-134.

Magurran, A.E., 2003. Measuring Biological Diversity. Blackwell Science Ltd, Oxford.

Magurran, A.E., McGill, B.J., 2011. Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford.

Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. Ecol. Appl. 22, 1535-1546.

Marc, P., Canard, A., Ysnel, F., 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agric. Ecosyst. Environ. 74, 229-273.

Marshall, E.J.P., 2009. The impact of landscape structure and sown grass margin strips on weed assemblages in arable crops and their boundaries. Weed Res. 49, 107-115.

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science 277, 504-509.

Millenium Ecosystem Assessment, 2005. Ecosystem and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Moon, K., Marshall, N., Cocklin, C., 2012. Personal circumstances and social characteristics as determinants of landholder participation in biodiversity conservation programs. J. Environ. Manage. 113, 292-300.

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., Dorn, S., 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships. Biol. Conserv. 130, 604-615.

Nascimbene, J., Marini, L., Paoletti, M.G., 2012. Organic farming benefits local plant diversity in vineyard farms located in intensive agricultural landscapes. Environ. Manage. 49, 1054–1060.

Nieminen, M., Ketoja, E., Mikola, J., Terhivuo, J., Siren, T., Nuutinen, V., 2011. Local land use effects and regional environmental limits on earthworm communities in Finnish arable landscapes. Ecol. Appl. 21, 3162-3177.

Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conserv. Biol. 4, 355-364.

Nyffeler, M., Sunderland, K.D., 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. Agric. Ecosyst. Environ. 95, 579-612.

OECD, 2011. Agriculture Policy Monitoring and Evaluation 2011.

Oertli, S., Muller, A., Steiner, D., Breitenstein, A., Dorn, S., 2005. Cross-taxon congruence of species diversity and community similarity among three insect taxa in a mosaic landscape. Biol. Conserv. 126, 195-205.

Oppermann, R., Beaufoy, G., Jones, G., 2012. High Nature Value Farming in Europe. Verlag Regionalkultur.

Palmer, M.W., 1990. The estimation of species richness by extrapolation. Ecology 71, 1195-1198.

Paoletti, M.G., 1999a. The role of earthworms for assessment of sustainability and as bioindicators. Agric. Ecosyst. Environ. 74, 137-155.

Paoletti, M.G., 1999b Using bioindicators based on biodiversity to assess landscape sustainability. Agric. Ecosyst. Environ. 74, 1–18.

Paoletti, M.G., D'Incá, A., Tonin, E., Tonon, S., Migliorini, C., Petruzzelli, G., Pezzarossa, B., Gomiero, T., Sommaggio, D., 2010. Optimizing sampling of soil invertebrates as bio-

indicators in a natural area converted from agricultural use: The case study of Vallevecchia-Lugugnana in north-eastern Italy. J. Sustainable Agric. 34, 38 - 56.

Paoletti M.G., Sommaggio D., Petruzzelli G., Pezzarossa B., Barbafieri M., 1995. Soil invertebrates as monitoring tools for agricultural sustainability. Polskie Pismo Entomologiczne, 64, 113-122.

Peigne, J., Cannavaciuolo, M., Gautronneau, Y., Aveline, A., Giteau, J.L., Cluzeau, D., 2009. Earthworm populations under different tillage systems in organic farming. Soil Till. Res. 104, 207-214.

Pelosi, C., Bertrand, M., Capowiez, Y., Boizard, H., Roger-Estrade, J. 2009. Earthworm collection from agricultural fields: Comparisons of selected expellants in presence/absence of hand-sorting. Eur. J. Soil Biol. 45, 176-183.

Pelosi, C., Goulard, M., Balent, G., 2010 The spatial scale mismatch between ecological processes and agricultural management: do difficulties come from underlying theoretical frameworks? Agric. Ecosyst. Environ. 139, 455–462.

Perner, J., Malt, S., 2003. Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. Agric. Ecosyst. Environ. 98, 169-181.

Pfiffner, L., Luka, H., 2007. Earthworm populations in two low-input cereal farming systems. Appl. Soil Ecol. 37, 184-191.

Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science, 333, 1289-1291.

Platnick, N.I., 2009. The World Spider Catalog, version 10.0. American Museum of Natural History.

Postma-Blaauw, M.B., de Goede, R.G.M., Bloem, J., Faber, J.H., Brussaard, L., 2010. Soil biota community structure and abundance under agricultural intensification and extensification. Ecology 91, 460-473.

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. Nature 405, 212–219.

Purvis, G., Curry, J.P., 1984. The influence of weeds and farmyard manure on the activity of carabidae on other gruond-dwelling arthropods in a sugar beet crop. J. Appl. Ecol. 21, 271-283.

Pysek, P., Jarosik, V., Kropac, Z., Chytry, M., Wild, J., Tichy, L., 2005. Effects of abiotic factors on species richness and cover in central european weed communities. Agric. Ecosyst. Environ. 109, 1-8.

R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria, http://cran.r-project.org.

R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org.

Rassam, G., Latifi, N., Soltani, A., Kamkar, B., 2011. Impact of crop management on weed species diversity and community composition of winter wheat fields in Iran. Weed Biol. Manage. 11, 83-90.

Raunkiær, C., 1934. The Life Forms of Plants and Statistical Plant Geography. Clarendon Press, Oxford.

Richner N., Holderegger R., Walter T., Linder P. (submitted to Biol. Conserv.). Phylogenetic structure in agricultural plant communities in Switzerland.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157-176.

Rudel, T. K., Defries, R., Asner, G. P., Laurance, W. F., 2009. Changing drivers of deforestation and new opportunities for conservation. Conserv. Biol. 23, 1396–1405.

Sachs, J.D., Baillie, J.E.M., Sutherland, W.J., Armsworth, P.R., Ash, N., Beddington, J., Blackburn, T.M., Collen, B., Gardiner, B., Gaston, K.J., Godfray, H.C.J., Green, R.E., Harvey, P.H., House, B., Knapp, S., Kumpel, N.F., Macdonald, D.W., Mace, G.M., Mallet, J., Matthews, A., May, R.M., Petchey, O., Purvis, A., Roe, D., Safi, K., Turner, K., Walpole, M., Watson, R., Jones, K.E., 2009. Biodiversity conservation and the millennium development goals. Science, 325, 1502-1503.

Samu, F., Sunderland, K., Szinetar, C., 1999. Scale-dependent dispersal and distribution patterns for spiders in agricultural systems: a review. The Journal of Arachnology, 27, 325-332.

Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.M., Bieringer, G., Milasowszky, N., Moser, D., Plutzar, C., Pollheimer, M., Storch, C., Trostl, R., Zechmeister, H., Grabherr, G., 2004. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. Biol. Conserv. 117, 181-190.

Schmidt-Entling, M.H., Dobeli, J., 2009. Sown wildflower areas to enhance spiders in arable fields. Agric. Ecosyst. Environ. 133, 19-22.

Schmidt, M.H., Roschewitz, I., Thies, C., Tscharntke, T., 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. J. Appl. Ecol. 42, 281-287.

Schmidt, M.H., Thies, C., Nentwig, W., Tscharntke, T., 2008. Contrasting responses ofarable spiders to the landscape matrix at different spatial scales. J. Biogeogr. 35,157–166.

Schmidt, M.H., Tscharntke, T., 2005. The role of perennial habitats for central European farmland spiders. Agric. Ecosyst. Environ. 105, 235-242.

Schuldt, A., Assmann, T., 2010. Invertebrate diversity and national responsibility for species conservation across Europe - a multi-taxon approach. Biol. Conserv. 143, 2747-2756.

Schweiger, O., Maelfait, J.-P., Van Wingerden, W.K.R.E., Hendricks, F., Billeter, R., Speelmans, M., Augenstein, I., Aukema, B., Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M., Bugter, R., 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. J. Appl. Ecol. 42, 1129-1139.

Siebert, R., Toogood, M., Knierim, A., 2006. Factors affecting European farmers' participation in biodiversity policies. Sociol. Rural. 46, 318-340.

Singh, M., Marchis, A., Capri, E., 2014. Greening, new frontiers for research and employment in the agro-food sector. Sci. Total Environ. 472, 437-443.

Smith, B., Wilson, J.B., 1996. A consumer's guide to evenness indices. Oikos 76, 70-82.

Socher, S.A., Prati, D., Boch, S., Muller, J., Klaus, V.H., Holzel, N., Fischer, M., 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology, 100, 1391-1399.

South, A., 2011. rworldmap: A New R package for Mapping Global Data. R J. 3.

SR-910.14, 2001. Ordinance on Environmental Quality. Systematic collection of Swiss Federal Laws, Bern.

Steffan-Dewenter, I., 2003. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Conserv. Biol. 17, 1036-1044.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83, 1421-1432.

Steffan-Dewenter, I., Tscharntke, T., 2001. Succession of bee communities on fallows. Ecography, 83-93.

Stolze, M., Lampkin, N., 2009. Policy for organic farming: rationale and concepts. Food Policy 34, 237–244.

Su, J.C., Debinski, D.M., Jakubauskas, M.E., Kindscher, K., 2004. Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conserv. Biol. 18, 167-173.

Sullivan, S., McCann, E., deYoung, R., Erickson, D., 1996. Farmers' attitudes about farming and the environment: a survey of conventional and organic farmers. J. Agric. Environ. Ethic. 9, 123-143.

Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annu. Rev. Entomol. 47, 561-594.

Tasser, E., Sternbach, E., Tappeiner, U., 2008. Biodiversity indicators for sustainability monitoring at municipality level: an example of implementation in an alpine region. Ecol. Indic. 8, 204 – 223.

Targetti, S., Herzog, F., Geijzendorffer, I.R., Wolfrum, S., Arndorfer, M., Balázs, K., Choisis, J.-P., Dennis, P., Eiter, S., Fjellstad, W., Friedel, J.K., Jeanneret, P., Jongman, R.H.G., Kainz, M., Lüscher, G., Moreno, G., Zanetti, T., Sarthou, J.-P., Stoyanova, S., Bailey, D., Paoletti, M.G., Viaggi, D., 2014. Estimating the cost of different strategies for measuring farmland biodiversity: evidence from a Europe-wide field evaluation. Ecol. Indic. (in press). doi: 10.1016/j.ecolind.2014.04.050

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151, 53–59.

Tscharntke, T., Gathmann, A., Steffan-Dewenter, I., 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. J. Appl. Ecol. 35, 708-719.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8, 857-874.

Tscharntke, T., Tylianakis, J., M., Rand, T., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W.,

Lindenmayer, D., Scherber, C., Navjot, S., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012b. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biological Reviews, 87, 661-685.

Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. J. Appl. Ecol. 51, 746-755.

Tuomisto, H., 2010. A consistent terminology for quantifying species diversity? Yes, it does exist. Oecologia 164, 853-860.

Tuomisto, H., Ruokolainen, K., 2006. Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. Ecology 87, 2697-2708.

van Eekeren, N., Bommele, L., Bloem, J., Schouten, T., Rutgers, M., de Goede, R., Reheul, D., Brussaard, L., 2008. Soil biological quality after 36 years of ley-arable cropping, permanent grassland and permanent arable cropping. Appl. Soil Ecol. 40, 432-446.

van Elsen, T., 2000. Species diversity as a task for organic agriculture in Europe. Agric. Ecosyst. Environ. 77, 101-109.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer.

Wagner, H.H., Edwards, P.J., 2001. Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. Landsc. Ecol. 16, 121-131.

Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyorgyi, H., Tscheulin, T., Vaissiere, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Mono., 78, 653-671.

Weyman, G.S., Sunderland, K.D., Jepson, P.C., 2002. A review of the evolution and mechanisms of ballooning by spiders inhabiting arable farmland. Ethol. Ecol. Evol. 14, 307-326.

Whitehorn, P.R., O'Connor, S., Wackers, F.L., Goulson, D., 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science 336, 351-352.

Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tscharntke, T., Weisser, W.W., Bommarco, R., 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. J. Appl. Ecol., 48, 570-579.

Worthen, W.B., 1996. Community composition and nested-subset analyses: Basic descriptors for community ecology. Oikos 76, 417-426.

Zurbuchen, A., Landert, L., Klaiber, J., Muller, A., Hein, S., Dorn, S., 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. 143, 669-676.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer.

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Publications

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Lüscher, G., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Bailey, D., Herzog, F., Pointereau, P., Richner, N., Jeanneret, P., 2014. Appropriate metrics to inform farmers about species diversity. Env. Sci. Pol. 41, 52-62.

Schneider, M.K., Lüscher, G., Jeanneret, P., Arndorfer, M., Ammari, Y., Bailey, D., Balázs, K., Báldi, A., Choisis, J.-P., Dennis, P., Eiter, S., Fjellstad, W., Fraser, M., Frank, T., Friedel, J., Garchi, S., Geijzendorffer, I.R., Gomiero, T., Gonzales-Bornay, G., Hector, A., Jerkovich, G., Jongman, R., Kakudidi, E., Kainz, M., Kovács-Hostyánszki, A., Moreno, G., Nkwiine, C., Opio, J., Oschatz, M.-L., Paoletti, M.G., Pointereau, P., Pulido, F.J., Sarthou, J.-P., Siebrecht, N., Sommaggio, D., Turnbull, L.A., Wolfrum, S., Herzog, F., 2014. Gains to species diversity in organically farmed fields are not propagated at the farm level. Nature Communications (in press).

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Presentations

Lüscher, G., Schneider, M.K., Jeanneret, P., 2011. Cross-taxon congruence of six species groups in European farmland. 41st Annual Meeting "Ecological Functions, Patterns, Processes", Ecological Society of Germany, Austria and Switzerland (GfÖ), Oldenburg, Germany, 5 – 9 Sep.

Lüscher, G., 2012. A closer look at species indicators. International Conference - Biodiversity Indicators for European Farming Systems, Engelberg, Switzerland, 21 – 22 Jun.

Lüscher, G., 2012. Species diversity in grassland and arable fields across Europe. 12th Congress of the European Society for Agronomy, Helsinki, Finland, 20 – 24 Aug.

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